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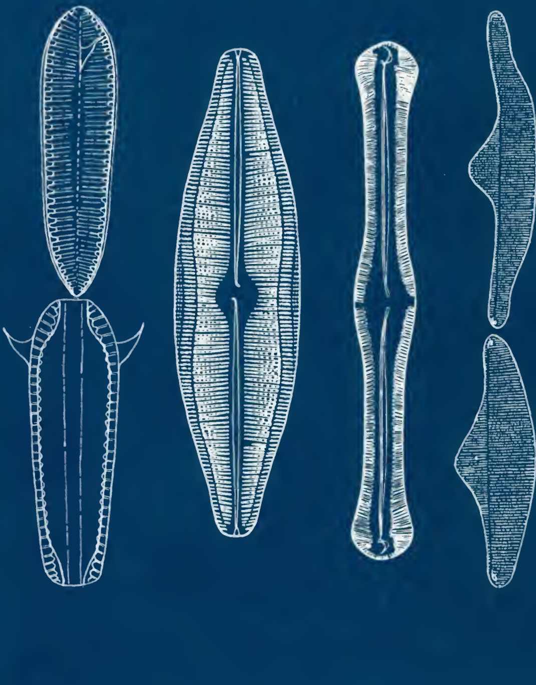

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*Diatom shells depicted on the front cover are intricately ornamented silicon (glass) coverings, or "walls" of single celled microscopic plants. Classification of diatoms has long been based on shell size, shape and (particularly) ornamentation. The two specimens on the left (*Surierella palmeri *Boyer) and the two on the right (*Eunotia stevensonii *Boyer) were first discovered and described by the well-known Academy diatomist Charles S. Boyer, who named them in honor of his early 20th century contemporaries. The center two diatoms (left to right) bear the names* Neidium boyeri *Reimer and* Pinnularia boyeri *Patrick, named in honor of C. S. Boyer by two of his successors at the Academy of Natural Sciences.*

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Otte, D. 1989. Speciation in Hawaiian crickets. pp. 482-526 *In* Otte, D. and J.A. Endler (eds.), Speciation and its Consequences. Sinauer Associates, Inc., Sunderland, MA. 679 pp.

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Systematics of Lizards of the Genus *Stenocercus* (Iguania:Tropiduridae) From Northern Perú: New Species and Comments on Relationships and Distribution Patterns

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ABSTRACT.— Five new species of iguanian lizards are described from the Andes and inter-Andean valleys of northern Perú. They are assigned to the genus *Stenocercus* Duméril and Bibron pending resolution of the status of that genus vis-a-vis *Ophryoessoides* Duméril and *Proctotretus* Duméril and Bibron. Species of *Ophryoessoides* are considered members of the genus *Stenocercus* sensu lato. Extensive descriptions and comparisons to other species in the genus are made to facilitate future work on this group, and amended descriptions are given for *Stenocercus simonsi* Boulenger and *S. carrioni* Parker. Some characters, such as neck folds and dermal mite pockets have been inadequately characterized in *Stenocercus*; standard descriptions are provided for these to facilitate comparisons. *Stenocercus percultus*, new species, is known from four areas along the Pacific versant of the Cordillera Occidental between the Río Zaña in the south and the upper Río Canchaque-Río Pusmalca (Depto. Piura) in the north, and from about 800m to about 1600m elevation. *Stenocercus percultus*, a large, strongly sexually dimorphic, species (males to 105mm snout-vent length), has deep posthumeral and postfemoral pockets; large, imbricate, keeled dorsal scales; keeled or multicarinate head scales; keeled, imbricate scales on the posterior surface of the thigh; and a high, serrate dorsal crest in males. It is similar to several species of *Stenocercus* of southern Ecuador and northern Perú: *ornatus*, *iridescens*, *rhodomelas*, *festae*, and *huancabambae* new species. *Stenocercus huancabambae* is known from localities below 1000m in the inter-Andean valleys of the upper Río Marañon and its tributaries in the Huancabamba Deflection region of northern Perú. It is a large species (males to 95mm snout-vent length) with deep posthumeral and postfemoral pockets; large, imbricate, keeled dorsal scales; keeled or multicarinate head scales; an enlarged row of supraoculars; a pair of projecting, blade-like, angulate temporal scales; and an extremely compressed tail in adult males. It is similar to other *Stenocercus* species of northern Perú and southern Ecuador: *percultus*, *iridescens*, *aculeatus*, and *scapularis*. *Stenocercus imitator*, new species, is described on the basis of specimens from several populations along the Pacific versant of the Cordillera Occidental in northern Perú between the Río Zaña in the south and the upper Río Canchaque-Río Pusmalca (Depto. Piura) in the north. These populations have previously been assigned to *S. praeornatus*, a species of the Amazonian versant in central Perú. *Stenocercus imitator* is strongly sexually dimorphic; either lacks or has an inconspicuous posthumeral pocket; has a deep postfemoral pocket; has smooth or slightly rugose head scales; and has granular lateral body scales. *Stenocercus eunetopsis*, new species, is known only from the vicinity of the type locality (about 1km SSW Udima, 2500m, Río Zaña, Depto. Cajamarca). It is a relatively small species (males to 83mm snout-vent length) characterized by weakly developed posthumeral and postfemoral pockets; little sexual dimorphism; small, smooth head scales; and a

rounded tail with large, strongly keeled scales bearing projecting spines. *Stenocercus eunetopsis* is most similar to *S. simonsi* of southern Ecuador. *Stenocercus chlorostictus*, new species, is known from the type locality (El Chorro, 1km N Monte Seco, 1300m, Río Zaña, Depto. Cajamarca) and from the vicinity of Canchaque (Depto. Piura, Perú). It is a small species (males to 75mm snout-vent length) having a spinose tail and weakly developed postfemoral pocket, but lacking posthumeral pockets and a projecting vertebral crest. *Stenocercus chlorostictus* is essentially identical to *S. carrioni* of southern Ecuador in all standard scutellational features, but differs in being strongly sexually dichromatic (males primarily green dorsally, females primarily brown) and in having a bold black antehumeral collar in males.

Females of *S. percultus* and *S. imitator* from the Río Zaña valley and the Abra de Porculla had enlarged ova during the dry season (May-August). Females of *S. eunetopsis* from the Río Zaña valley had enlarged ova at the beginning of the dry season (May-June), but one female with enlarged ova was also collected in January. Known clutch sizes for these species are: *percultus* (2), *eunetopsis* (2), and *imitator* (4-5).

The type locality for *Stenocercus boettgeri* Boulenger (and other species described by Boulenger from the Boettger collection) is Huancabamba, Depto. Pasco, Perú, not the Huancabamba of Depto. Piura, Perú, as reported in recent literature. Boulenger's report of specimens of *S. simonsii* from near the city of Cajamarca, Perú is based on specimens of *S. empetrus*. *Stenocercus empetrus* is known from the high valleys on the western side of the Río Marañon and from the adjacent crest of the Cordillera Occidental; a specimen of this species reportedly from Otuzco (Depto. Cajamarca, Pacific versant, 2650m) very likely comes from higher mountains to the north and west.

Characteristics of several of the described species suggest their relationships with species of southwestern Ecuador: *S. eunetopsis* with *S. simonsi* Boulenger; *S. chlorostictus* with *S. carrioni* Parker; and *S. percultus* with *S. rhodomelas* and *S. ornatus*. The relationships of *S. huancabambae* are unclear, but it shares some features with *S. aculeatus* and other species usually referred to *Ophryoessoides*. If *Stenocercus imitator* is closely related to *S. praeornatus*, it is the only species of the Pacific versant described here for which there is a hypothesized close relationship to species of the Amazonian versant.

On the Pacific versant of the Andes in northern Perú species of *Stenocercus* are elevationally stratified, with no more than three species known to be sympatric. *Stenocercus percultus*, *S. chlorostictus*, and *S. imitator* are sympatric in the vicinity of Monte Seco (Río Zaña, Depto. Cajamarca) and the vicinity of Canchaque (Depto. Piura). They are representative of a distinctive fauna inhabiting relictual humid forests on the western versant of the Cordillera Occidental. *Stenocercus huancabambae* is not known to be sympatric with other species of *Stenocercus*. *Stenocercus eunetopsis* is sympatric with *S. imitator*.

Few species of *Stenocercus* are known from intermediate elevations of both Pacific and Amazonian versants, and most of these occur in the low intermontane basins of southern Ecuador. The Huancabamba Deflection region represents a strong biogeographic discontinuity for *Stenocercus*. No species of *Stenocercus* is known to occur both north and south of this area, although it is a region of high species diversity for the genus.

Both intra- and interspecific variation for presence/absence of pterygoid teeth in *Stenocercus* are documented, but this is not obviously correlated with either ontogeny or sex. However, samples are not generally adequate to evaluate the pattern of variation in this character.

[Andes, distribution, Ecuador, Iguania, Iguanidae, lizard, new species, *Ophryoessoides*, Peru, South America, *Stenocercus*, Squamata, systematics, Tropiduridae]

RESUMEN.— Se decriben cinco nuevas especies de lagartijas iguanianas de los Andes y los valles interandinos del norte de Perú. Ellos se asignan al género *Stenocercus* Duméril y Bibron hasta la resolución de las relaciones entre *Stenocercus* y los géneros *Ophryoessoides* Duméril y *Proctotretus* Duméril y Bibron. Las especies de *Ophryoessoides* se consideran miembros del género *Stenocercus* sensu lato. Se hacen descripciones y comparaciones amplias a otras especies de *Stenocercus* para facilitar trabajo con este grupo complicado. Se dan descripciones enmendadas para *Stenocercus simonsi* Boulenger y *Stenocercus carrioni* Parker. Algunos caracteres, por ejemplo los pliegues del cuello y

los bolsillos acáridos no se han sido bien caractizado. Se proveen descripciones estandardizadas para ellos para facilitar comparaciones. *Stenocercus percultus*, nueva especie, se conoce de cuatro regiones de la vertiente pacífica de la Cordillera Occidental entre el Río Zaña al sur y el alto Río Canchaque-Río Pusmalca (Depto. Piura) al norte, y desde 800m y 1600m de altura. *Stenocercus percultus*, una especie grande con dimorfismo sexual marcado (los machos hasta 105mm de longitud corporal), tiene profundos bolsillos posthumerales y postfemorales; escamas dorsales grandes, imbricadas, y quilladas; escamas de la cabeza quilladas o arrugadas; escamas quilladas y imbricadas sobre el aspecto posterior del muslo; y una cresta alta y serrada en los machos. Esta especie es similar a varios especies de *Stenocercus* del sur de Ecuador y el norte de Perú: *ornatus*, *iridescens*, *rhodomelas*, *festae*, y *huancabambae* nueva especie. Se conoce *Stenocercus huancabambae* de localidades por debajo de 1000 m en los valles interandinos del alto Río Marañon y sus afluentes en la región de la Deflección de Huancabamba en el norte de Perú. Es una especie grande (los machos hasta 95 mm de longitud corporal) con bolsillos posthumerales y postfemorales profundos; escamas dorsales grandes, imbricadas, y quilladas; escamas quilladas o arrugadas sobre la cabeza; una hilera de escamas supraoculares grandes; un par de escamas temporales en forma de cuchilla; y una cola sumamente comprimido en machos adultos. Es una especie similar a otras del norte de Perú y el sur de Ecuador: *percultus*, *iridescens*, *aculeatus*, y *scapularis*. Se describe *Stenocercus imitator*, nueva especie, basado en especimenes de varias poblaciones de la vertiente pacífica de la Cordillera Occidental del norte de Perú entre el Río Zaña al sur y el alto Río Canchaque-Río Pusmalca (Depto. Piura) al norte. Estas poblaciones han sido consideradas miembras de la especie *S. praeornatus*, la cual es conocida de la vertiente amazonica de Perú central. *Stenocercus imitator* tiene dimorfismo sexual marcado; o tiene o carece de un bolsillo posthumeral discreto; tiene un bolsillo postfemoral profundo; tiene escamas lisas o poca rugosas sobre la cabeza; y tiene escamas granulares sobre la parte lateral del cuerpo. Se conoce *Stenocercus eunetopsis*, nueva especie, solamente de la vecinidad de la localidad típica (aproximadamente 1km sur sur oeste de Udima, 2500m, Río Zaña, Depto. Cajamarca). Es una especie algo pequeña (los machos hasta 83mm de longitud corporal) caracterizada por bolsillos posthumerales y postfemorales debilmente desarollados; poco dimorfismo sexual; escamas pequeñas y lisas sobre la cabeza; y una cola redonda que lleva escamas grandes y fuertamente quilladas con espinas resaltandas. *Stenocercus simonsi* del sur de Ecuador es la especie más similar a *S. eunetopsis*. *Stenocercus chlorostictus*, nueva especie, es conocido de la localidad típica (El Chorro, 1km al norte de Monte Seco, 1300m, Río Zaña, Depto. Cajamarca) y de la vecinidad de Canchaque (Depto. Piura). Es una especie pequeña (los machos hasta 75mm de longitud corporal) con una cola espinosa y un bolsillo postfemoral debilmente desarollado, pero no tiene ni un bolsillo posthumeral ni cresta vertebral resaltada. En características de la escamación, *Stenocercus chlorostictus* es casi idéntica a *S. carrioni* del sur de Ecuador, pero difere al tener dimorfismo sexual marcado en los colores (los machos principalmente verdes, las hembras principalmente marrones), y al tener un collar negro pronunciado en los machos.

Hembras de *S. percultus* y *S. imitator* del valle del Río Zaña y la Abra de Porculla tenía óvulos aumentos durante la estación seca (Mayo hasta Agosto). Hembras de *S. eunetopsis* del valle del Río Zaña tenía óvulos aumentos a principios de la estación seca (Mayo hasta Júnio), pero una hembra con óvulos aumentos se colectaba en enero. El tamaño de las nidadas de estas especies son: *percultus* (2), *eunetopsis* (2), y *imitator* (4 o 5).

La localidad típica de *Stenocercus boettgeri* Boulenger (y otras especies descritas por Boulenger de la colección de Boettger) es Huancabamba, Depto. Pasco, Perú, no la Huancabamba del departamento de Piura, Perú, como relatado en la literatura reciente. El reporte de Boulenger de *Stenocercus simonsi* cercano la ciudad de Cajamarca, Perú, es basado en especimenes de *S. empetrus*. Se conoce *Stenocercus empetrus* de los valles altos del lado oeste del Río Marañon en los deparamentos de Cajamarca y La Libertad, y de la cima adyacente de la Cordillera Occidental; un ejemplar de esta especie dicho a ser de Otuzco (Depto. Cajamarca, vertiente pacífica, 2650m) probablemente se colectaba en las montañas altas al norte y oeste.

Características de varias especies descritas indican sus relaciones con especies del suroeste de Ecuador: *S. eunetopsis* con *S. simonsi* Boulenger; *S. chlorostictus* con *S. carrioni* Parker; y *S. percultus* con *S. rhodomelas* y *S. ornatus*. Las relaciones de *Stenocercus huancabambae* no estan claras, pero el

tiene características en común con *S. aculeatus* y otras especies referidas al género *Ophryoessoides*. Si *Stenocercus imitator* es cercanamente relacionada a *S. praeornatus*, es la única especie descrita de la vertiente pacífica que posiblemente tiene relaciones cercanas con especies de la vertiente amazónica.

En la vertiente pacífica de los Andes al norte de Perú, especies de *Stenocercus* son estratificadas segun la elevación, y no hay más que tres especies simpátricas. *Stenocercus percultus*, *S. chlorostictus*, y *S. imitator* son simpátricos en la vecinidad de Monte Seco (Río Zaña, Depto. Cajamarca) y en la vecinidad de Canchaque (Depto. Piura). Ellos representan una fauna distintiva de los bosques húmedos reliquiales de la vertiente oeste de la Cordillera Occidental. No se conoce localidades donde *Stenocercus huancabambae* es simpátrico con otras especies de *Stenocercus*. *Stenocercus eunetopsis* es simpátrico con *S. imitator*.

Se conocen pocas especies de Stenocercus de las elevaciones intermedias de tanto la vertiente pacífica como la vertiente amazónica. La mayoría de estas ocurre en las cuencas bajas intermontanas del sur de Ecuador. La región de la Deflección de Huancabamba es una discontinuidad biogeográfica bien marcada para *Stenocercus*. No ocurre ninguna especie tanto al norte como al sur de esta región, aunque es una región de alta diversidad para el género.

Se documenta variación intraespecífica y interespecífica en la presencia o ausencia de dientes pterygoidos en *Stenocercus*, pero la variación no corresponde evidentamente con la ontogenia o el sexo. Sin embargo, las muestras osteológicas no son adecuadas para evaluar el patrón de variación de esta carácter.

Stenocercus is one of many genera of South American iguanian lizards whose systematics is poorly understood. Fritts (1974) gave a brief characterization of the species of *Stenocercus* (excluding some which he referred to the genus *Ophryoessoides*, about which more will be said below). However, there has been no detailed treatment, and the relatively rapid rate of discovery of new species indicates that much basic work remains before we gain a reasonably comprehensive understanding of this genus. Because of this, species limits and their distributions remain poorly characterized, hampering biogeographic and phylogenetic studies on this diverse group of South American lizards.

The literature on *Stenocercus* poses difficulties for anyone attempting to identify with certainty the species to which particular population samples may pertain. In part, this is owing to the many rather brief descriptions found in earlier species accounts, and an unknown, but sizable, number of undescribed taxa. Fritts' (1972) description of seven Peruvian species increased the number of taxa known from Perú by about 50%. The discovery of four new Peruvian species at a single (relatively accessible) site, which forms the basis of this report, suggests that many others may await discovery. Moreover, during this investigation specimens were found in museum collections whose identity was clearly questionable, and specimens in many collections remain unstudied; some specimens from earlier collections in northern Perú are representative of another species described as new herein. No species of *Stenocercus* has been subjected to a thorough study of geographic variation (indeed, many are known from relatively few localities), which frustrates attempts to assign some outlying populations to species already described, or to new taxa.

In this paper I describe five species of *Stenocercus* as part of a series of taxonomic treatments of the herpetofauna of the western Andes in northern Perú (Cadle 1989, Cadle and McDiarmid 1990). My field work has centered on the herpetofauna in the vicinity of Hacienda Monte Seco at about 1200m elevation in the Río Zaña valley, a west-facing valley of the Cordillera Occidental in extreme western Cajamarca department, Perú; collections from

this local area span the elevational range from about 1200m to about 3000m. One of the new species of *Stenocercus* is known only from the Río Zaña valley. Three others are known from the Río Zaña valley and other sites on the Pacific versant of the Cordillera Occidental in northern Perú. The fifth new species is known from the dry upper Marañon interandean valleys in the Huancabamba Deflection region of northern Perú (Amazonian versant), and was first collected by G. K. Noble in the early part of this century. In describing these species, I have found it necessary to provide amended descriptions of two species, *Stenocercus simonsi* Boulenger and *S. carrioni* Parker, to aid in distinguishing them from some of the new species.

My approach in describing species herein has been to present exhaustive characterizations and comparisons to other species of *Stenocercus*, details which are too frequently lacking in many of the original descriptions. These detailed descriptions should facilitate comparisons with newly discovered populations or species, and hopefully will promote a better comprehension of character variation within the genus, leading ultimately to the thorough revision needed for *Stenocercus*. Geographic variation is characterized and discussed where appropriate. In the comparisons I have relied heavily on original descriptions in addition to examination of new material (see Appendix), and I have used information from Fritts' (1974) summary of the then-known species. Users of the older literature are cautioned, however, that adequate characterization of intraspecific variation does not accompany many earlier accounts, and many subtle differences among species are inadequately described because of vague or imprecise terminology used for particular characters. I have endeavored to provide a more precise terminology for features such as the neck folds and dermal mite pockets.

GENERIC STATUS OF FORMS DESCRIBED HEREIN

The generic allocation for the species described herein is tentative. Assignment to the genus *Stenocercus* Duméril and Bibron, 1837, is provisional and must remain so until considerably more revisionary work on *Stenocercus* and the related genera *Ophryoessoides* Duméril, 1851, and *Proctotretus* Duméril and Bibron, 1837, is accomplished. These three genera have been recognized as related by many workers (e.g., Etheridge, 1966; Fritts, 1974; Etheridge and de Queiroz 1988). For many years they have been considered part of a larger informal group of iguanians, the tropidurines, or *Tropidurus* group (e.g., Etheridge and de Queiroz 1988; Williams 1988). They were placed in the Tropiduridae by Frost and Etheridge (1989), who raised many previously informally-recognized groups within Iguania to family level. Frost (1988) considered *Stenocercus*, *Ophryoessoides*, and *Proctotretus* a tribe (Stenocercini) of the Tropiduridae.

Prior to Etheridge's (1966) work many of the mainland South American species presently referred to *Stenocercus* and *Ophryoessoides* were placed, along with about 15 species from the West Indies, in the genus *Leiocephalus* Gray, 1827. Etheridge (1966) separated the continental from the West Indian species of *Leiocephalus*, placing the former in the genus *Ophryoessoides*. He recognized the possible association of some species of the expanded *Ophryoessoides* with species of *Stenocercus*, but deferred exploration of that possibility pending further study of *Stenocercus*. Fritts (1974) redefined both genera and reallocated many taxa of *Ophryoessoides* to *Stenocercus*. Based on external criteria, he referred those species with enlarged supraocular scales, large posterior head scales, large imbricate dorsal scales, keeled ventrals, and relative long or laterally-compressed tails to *Ophryoessoides*, and species with small supraoculars, small posterior head scales, small dorsals, and with relatively short rounded tails to *Stenocercus*. Those species included in

Ophryoessoides by Fritts (1974) are *aculeatus* (O'Shaughnessy), *caducus* (Cope), *erythrogaster* (Hallowell), *iridescens* (Gunther), *scapularis* (Boulenger), and *tricristatus* Duméril. Of these, *iridescens* is from Pacific coastal Ecuador and Perú, *erythrogaster* is from the Andes of Colombia, and the remaining species are from cis-Andean South America. Fritts (1974) included 29 species in *Stenocercus*, and one additional species was described y Castro and Ayala (1982).

Frost (1992), in a phylogenetic analysis of South American iguanians, suggested that *Stenocercus* was paraphyletic with respect to *Ophryoessoides*, which he therefore considered a junior synonym of *Stenocercus*. Although *Proctotretus* is demonstrably monophyletic, Frost (1988) indicated that *Stenocercus* (including *Ophryoessoides*) was possibly paraphyletic with respect to it. Pending resolution of these taxonomic problems, I follow Frost's recommendation that *Ophryoessoides* be considered a junior synonym of *Stenocercus*, and allocate the species described herein to *Stenocercus*. However, I consider all species of the nominal genera *Stenocercus* and *Ophryoessoides* as recognized by Fritts (1974). For each species, I provide a brief series of diagnostic features, but also an extensive series of comparisons, to facilitate identifications and future revisionary work.

MATERIALS AND METHODS

Measurements and Scale Counts

All measurements are in millimeters. Abbreviations: SVL, snout to vent length; TAL, tail length; TOL, total length; HL, head length, measured with dial calipers from the snout tip to the anterior border of the ear; HW, head width, measured with dial calipers at the angle of the jaw.

Because of irregularities in the pattern of scale distribution in *Stenocercus*, body scale counts (midbody, vertebrals, paravertebrals, gulars) are somewhat imprecise. However, they are repeatable within narrow limits (generally $\pm$2 to 4 scales, for example, at midbody). They are useful for giving an indirect measure of relative scale size among species. The following scale counts and associated terminology were used: (1) **Midbody scales**, counted in a vertical plane midway between the limbs. (2) **Vertebral scales**, either those of the dorsal crest, when present, or along the undifferentiated vertebral row from the occipital scales to a point in line with the posterior edge of the thigh when extended perpendicular to the body. In some species, the vertebral row is indistinguishable from adjacent scale rows, whereas in others it is enlarged and sometimes more strongly keeled than adjacent rows. The vertebral crest is said to be **projecting** when there is a vertical vane extending distinctly above the plane of middorsal scale rows. (3) **Paravertebral scales**, counted on the scale row adjacent to the vertebral row from the occipital region to a point in line with the posterior edge of the thigh when extended perpendicular to the body. Paravertebral scales were counted only on species that possessed a differentiated vertebral scale row (dorsal crest), in which case the vertebral scales are larger than adjacent paravertebrals. The term **paradorsal scales** refers collectively to all scales of the dorsum between the vertebral row and the lateral body scales; these are often morphologically distinct from the lateral scales. (4) **Gular scales**, counted between the ventral edges of the ear openings, but not including tiny scales within the ear margin; a rule of thumb was to start and end the counts with the first enlarged scale ventral to the ear openings. (5) **Internasals**, the number of scales between the nasal scales, counted immediately posterior to the medial postrostrals (internasals occasionally contact the rostral, in which case they are distinguished from postrostrals by their antero-posteriorly elongate shape, in contrast to the transverse elongation of postrostrals). (6) **Angulate temporal scales** are one or more enlarged, keeled scales, roughly in line with the superciliary rows, and on the border between the lateral temporal scales and the posterior dorsal head scales (Fritts 1974:12; hence, "angulate," in reference to their position at the angle between

the dorsal and lateral head surfaces). In many species of *Stenocercus*, the scales in this region are not distinguished in size or keeling from adjacent posterior head scales or the lateral temporal scales. In other species, the scales are distinctly differentiated from adjacent lateral or dorsal head scales by being larger and more strongly keeled, and it is these differentiated scales that I refer to as *angulate temporals*. In a few species (apparently mostly species of *Ophryoessoides* sensu Fritts [1974]), the angulate temporals bear a projecting blade-like vane. These latter are the "erect scales forming a flag-like border" on each side of the occiput, and the "projecting scales" on the supratemporal edge, referred to by O'Shaughnessy (1881:243) and Boulenger (1885:167), respectively, in their descriptions of *S. aculeatus*. In my discussion, I refer to angulate temporals bearing such a blade-like vane as *projecting angulate temporals*. The vane apparently develops ontogenetically; in those species possessing projecting angulate temporals in adults, juveniles possess very strongly keeled, but not projecting, scales. Hence, interspecific comparisons of these scales should use specimens of similar size; unless otherwise stated, reference to these scales herein refer to the condition in larger adult specimens. The variability in the form of scales in this region among species of *Stenocercus* appears to be of systematic significance, but is inadequately analyzed presently. Scales differentiated as angulate temporals were not observed in any of ten species of *Leiocephalus* examined, in which the small lateral temporals meet the enlarged posterior head scales abruptly. (7) **Subdigital lamellae**, counted on the left side only on the 4th finger and the 4th toe (in cases of damage to the left side, counts on the right side were substituted). (8) **Scales around the base of the tail**, counted in a vertical plane just posterior to the vent (used only in characterizing one of the species described here). (9) **Supraocular scales** are here considered to comprise all scales on the dorsal surface of the orbit, whether enlarged or not. In species in which there is a row of distinctly enlarged supraoculars, the term "circumorbitals" is sometimes used for the small rows of supraoculars separating the enlarged supraoculars from median head scales (e.g., Smith 1946:21; Frost 1992); I do not use that term here because it could be consistently applied to only one of the species under consideration. The supraoculars were counted in a transverse line across the greatest width of one of the orbits. (10) **Supraorbital semicircles** are used in the sense of Smith (1946:20) and Peters (1964, definition 2) for the scales bordering the supraoculars between the canthal ridge and the posterior border of the orbit.

Summaries of scale counts and qualitative features for new species are given in Table 1. They are not generally repeated in the characterizations of those taxa in the species accounts, but they should be considered integral parts of the accounts. Scale counts and qualitative features for other species considered in detail in this paper are also summarized in Table 1, and they are considered in the comparisons for each species in the species accounts. Geographic variation in scale counts is considered in each species account, where a breakdown for particular populations is given.

Neck Folds

I use the term "neck fold" collectively for all of the skin folds present on the lateral and ventral surfaces of the region between the forelimbs and the angle of the jaw (or continuing from this region onto the body). This is a broader usage than Fritts' (1974) term "neck fold" (which corresponds to the term "oblique neck fold" as used in this paper) but similar to Frost's (1988) more extensive discussion of these features. My terminology follows Frost (1988:161-171), whose work should be consulted for more extensive discussion. Figure 1 illustrates major neck folds in *Stenocercus*, which are characterized as follows:

Antehumeral fold — a more or less vertical or oblique fold extending across the scapular region.

Posthumeral fold — a fold extending obliquely downward from the dorsolateral fold behind the forelimb.

Table 1. Summary of selected meristic and qualitative characteristics of nine species of *Stenocercus*. For meristic characters and Tail/Total length ratios, the range, mean, standard deviation (in parentheses), and sample sizes are given. These values reflect combined population samples for each species. Geographic variation is considered in the species accounts.

	Stenocercus percultus new species	*Stenocercus huancabambae* new species	*Stenocercus imitator* new species	*Stenocercus eunetopsis* new species	*Stenocercus chlorostictus* new species
Midbody Scales	50-65 56.64 (3.79) 42	37-53 43.94 (3.20) 102	85-124 102.96 (8.31) 100	60-80 70.62 (5.38) 29	80-110 89.00 (12.69) 5
Midbody Scales	35-50 42.19 (3.26) 41	37-51 43.39 (3.40) 102	49-66 56.87 (3.44) 100	59-80 71.45 (5.42) 29	63-73 68.40 (3.58) 5
Paravertebral Scales	62-77 70.39 (3.73) 41	48-64 56.31 (3.74) 102	89-119 102.15 (6.39) 80	—[1]	—
Gular Scales	20-28 24.37 (1.84) 41	18-28 20.93 (1.64) 100	29-44 34.98 (2.97) 98	37-57 44.00 (4.75) 29	34-42 37.40 (3.13) 5
Internasal Scales	2-4 3.81 (0.46) 42	4-7 5.72 (0.49) 102	3-5 3.91 (0.36) 115	3-5 3.69 (0.54) 29	4 4.00 (0.00) 5
Supraocular Scales	4-6 4.96 (0.373) 42	3-6 4.73 (0.644) 102	4-7 5.58 (0.686) 98	4-8 5.48 (0.73) 29	5-6 5.90 (0.32) 5
4th Finger Subdigital Lamellae	17-22 19.55 (1.50) 42	14-20 16.81 (1.41) 102	19-26 22.95 (1.34) 100	22-27 23.62 (1.37) 29	20-26 24.20 (2.68) 5
4th Toe Subdigital Lamellae	24-32 27.54 (1.96) 41	20-28 24.62 (1.56) 102	28-37 32.60 (1.89) 100	28-35 31.17 (1.95) 29	24-32 27.60 (3.21) 5

continues on p. 10, 11

	Stenocercus praeornatus Fritts (part)	*Stenocercus simonsi* Boulenger	*Stenocercus empetrus* Fritts	*Stenocercus carrioni* Parker
Midbody Scales	99-122 107.67 (8.41) 6	79-102 94.20 (6.63) 20	86-111 95.78 (6.78) 27	66-96 82.43 (8.13) 21
Vertebral Scales	65-71 67.83 (2.56) 6	59-98 73.75 (9.76) 20	70-113 94.52 (9.27) 27	55-72 64.43 (5.18) 21
Paravertebral Scales	—	94-118 107.2 (9.02) 20	—	76-96 86.67 (5.36) 21
Gular Scales	38-50 46.50 (4.28) 6	36-57 49.26 (5.33) 19	40-54 46.00 (3.66) 27	37-52 46.48 (4.14) 21
Internasal Scales	4 4.00 (0) 6	4 4.00 (0) 19	3-4 3.67 (0.48) 27	4 4.00 (0) 21
Supraocular Scales	4-6 5.17 (0.52) 6	6-9 7.11 (0.76) 19	4-6 5.20 (0.49) 27	5-7 5.81 (0.56) 21
4th Finger Subdigital Lamellae	19-22 20.83 (1.33) 6	24-28 26.15 (1.23) 20	17-27 21.93 (2.15) 27	23-28 25.19 (1.25) 21
4th Toe Subdigital Lamellae	27-30 28.8 (1.30) 5	28-37 31.15 (2.46) 20	26-33 28.77 (1.86) 26	27-32 29.80 (1.44) 20

Table 1 (continued)

	Stenocercus percultus new species	*Stenocercus huancabambae* new species	*Stenocercus imitator* new species	*Stenocercus eunetopsis* new species	*Stenocercus chlorostictus* new species
Tail/Total Length	0.67-0.70 0.69 (0.01) 22	0.65-0.71 0.68 (0.01) 48	0.64-0.70 0.68 (0.01) 62	0.64-0.66	0.56-0.60 0.58 (0.02) 4
Maximum Size (mm)					
Males	105	95	100	83	75
Females	86	75	87	74	69
Posthumeral Pocket (adult males)	Type 4	Type 4	Type 1-2	Type 1-2	Type 1
Postfemoral Pocket (adult males)	Type 5	Type 5	Type 5	Type 2-3	Type 3
Tail[2]	Moderately to Strongly Compressed	Extremely Compressed	Moderately Compressed	Rounded Proximally; Very Spinose	Rounded; Moderately Spinose
Dorsal Head Scales	Keeled, Wrinkled or Multicarinate	Keeled or Multicarinate	Smooth to slightly rugose	Smooth	Smooth
Lateral neck Scales	Imbricate, Keeled	Imbricate, Keeled	Granular	Granular	Granular
Posterior Thigh Scales	Imbricate, Keeled	Imbricate, Keeled	Granular	Granular	Granular
Sexual Dimorphism Coloration/Pattern	Strong	Strong	Strong	Absent	Strong
Body Form	Strong	Strong	Strong	Size only	Size only

[1] In *S. eunetopsis* and *S. chlorostictus* the vertebral and paravertebral scale rows are subequal; hence, only counts for the former are given.

[2] In *S. percultus* and *S. huancabambae* the tail form is strongly dimorphic between the sexes. The listed form is for adult males. In females of both species the tails are less compressed and more rounded.

	Stenocercus praeornatus Fritts (part)	*Stenocercus simonsi* Boulenger	*Stenocercus empetrus* Fritts	*Stenocercus carrioni* Parker
Tail/Total Length	0.62-0.66 0.63 (0.02) 3	0.59-0.65 0.63 (0.01) 5	0.51-0.61 0.57 (0.03) 18	0.56-0.60 0.57 (0.01) 10
Maximum Size (mm)				
Males	100	88	96	74
Females	82	79	89	71
Posthumeral Pocket	Type 1-2	Type 1	Type 1	Type 1-2
Postfemoral Pocket	Type 5	Type 3	Type 2-3	Type 3
Tail	Rounded to Slightly Compressed	Compressed Distally; Very Spinose	Rounded	Rounded-Compressed; Spinose
Dorsal Head Scales	Smooth	Smooth	Smooth	Smooth-Wrinkled
Lateral Neck Scales	Granular	Granular	Granular	Granular
Posterior Thigh Scales	Granular	Granular	Granular	Granular
Sexual Dimorphism Coloration/ Pattern	Moderate/ Strong	Absent	Absent	Absent
Body Form	Strong	Size only	Size only	Size only

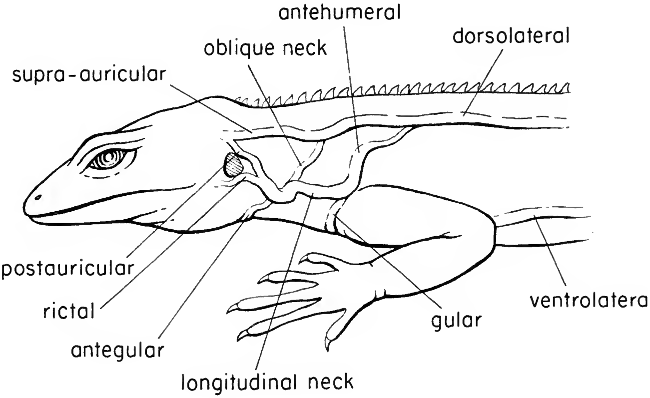

Fig. 1. Diagram of major neck folds in *Stenocercus*. The figure shows a relatively complete series of folds, based on the pattern in *Stenocercus imitator*, described herein. Drawn by L. Meszoly, used with permission of E. E. Williams.

Gular fold — a fold immediately in front of the forelimb and extending ventrally onto the neck; confluent with the antehumeral fold (if present) in the species considered here, and accompanied by strongly reduced scales. Although in many iguanians the gular fold is complete across the venter, in *Stenocercus* and related genera, it is incomplete midventrally (Etheridge and de Queiroz 1988, Frost 1988).

Dorsolateral fold — A fold extending for a variable length along the body, over the forelimb insertion to the antehumeral fold, with which it is usually confluent.

Ventrolateral fold — a fold ventrolaterally along the body posterior to the forelimb (thus, technically, not a "neck" fold).

Supra-auricular fold — A continuation of the dorsolateral fold between the antehumeral fold and the ear.

Oblique neck fold (= "neck fold" of Fritts 1974) — a fold more or less parallel to the antehumeral fold, usually about midway between the posterior border of the ear and the forelimb; often connected dorsally to the supra-auricular fold, and ventrally to the longitudinal neck fold. In one species described here, **supernumerary oblique neck folds**, in addition to the usual one, occur between the supra-auricular fold and the longitudinal neck fold.

Antegular fold — a fold across the ventral surface of the neck anterior to the gular fold; sometimes confluent with a ventral extension of the oblique neck fold. The antegular fold in species under consideration here is accompanied by several rows of scales reduced in size over adjacent rows of the neck.

Longitudinal neck fold — a ventrolateral longitudinal fold extending from the posteroventral edge of the ear to the forelimb. It is thus more or less parallel to the supra-auricular fold.

Postauricular fold — a fold immediately behind the ear; usually confluent with the longitudinal neck fold and the supra-auricular fold.

Rictal fold — a fold (weak in the species considered here) ventral and anteroventral to the ear (extends further anteriorly in some other lizards; see Frost 1992).

Posthumeral and Postfemoral pockets

Considerable variation in these structures, mostly unstudied and uncharacterized, exists among species of *Stenocercus*, as well as age, sex, and geographic variation within species. Although many descriptions of *Stenocercus* spp. note presence/absence of these structures (e.g., Castro and Ayala 1982) or describe their degree of development ("moderate," "weak," etc.; Fritts 1974), such characterizations obscure much of the complexity present in the structure of the pockets that may ultimately prove to be of great systematic value. A comprehensive study of this feature is beyond the scope of the present work; such a study should eventually be directed toward standardizing descriptions for variation in pocket structure for *Stenocercus* and related genera. Rodrigues (1987:108-113) and Frost (1992) described some of the variation present among tropidurids, but a comprehensive classificatory scheme is, as yet, lacking. For use herein, I devised an arbitary classification of five general forms for the species studied (based on the form in adult males). However, detailed descriptions for each species are given in the accounts. This classification is not intended to encompass the total range of variation in dermal pocket structure found within *Stenocercus* (a study not undertaken for the present work), nor to deal with the sometimes seemingly continuous variation between discrete types. However, as an adjunct to Fritts' (1974) less specific notes on these features, I indicate below the form of the pockets for the species in which I examined adult males. Note, however, that no attempt was made to assess intraspecific variation comprehensively; this should eventually be incorporated into a comprehensive survey of the whole genus. External views of two variations of Types 4 and 5 are illustrated in Figs. 2 and 3. The forms recognized are:

Type 1 (pocket absent) — no apparent skin modification.

Type 2 — noticeable skin modification such as bare patch of skin, a series of wrinkles in the skin, or a shallow depression lined with scales different from surrounding body scales.

Type 3 — as in Type 2, but with the addition of an overhanging fold of skin or thickened border; a shallow, but distinct, pocket. Depth generally less than half the diameter of the opening.

Type 4 (Figs. 2 and 3) — A moderate to deep pocket usually having a broad circular opening (opening sometimes narrow). Depth greater than half the diameter of the opening. Observed only in posthumeral pockets in the species studied (the postfemoral pocket of the single specimen of *S. orientalis* examined approaches this condition).

Type 5 (Figs. 2 and 3) — A moderate to deep pocket with a narrow, slit-like opening. Depth generally greater than half the greatest diameter of the opening. Observed only in postfemoral pockets in the species studied.

The distinction between Types 1 and 2 is sometimes quite subtle (and arbitary in such cases), owing to the difficulty of discerning whether a series of wrinkles in the axillary or postfemoral regions is, in fact, a discrete structure, or a result of preservation artifact. Often mites are present in these regions without salient skin modification; such cases were coded as Type 2. Some variation in scale ornamentation and pocket form occurs within Types 4 and 5 (Figs. 2 and 3), which I have not attempted to characterize further. With more extensive survey of variation in pocket structures using more specimens and broader taxonomic coverage, it will surely be possible to refine this crude system, which should be viewed as a first attempt to delineate the different pocket forms in *Stenocercus*.

The form of the pockets (adult males only) in the species of *Stenocercus* examined are as follows (in parentheses after each species name are listed the type of posthumeral pocket, type of postfemoral pocket): *aculeatus* (4, 3; the opening of the posthumeral pocket is quite narrow, although the pocket is deep); *boettgeri* (1-2, 3 or 5); *carrioni* (1-2, 3); *chrysopygus* (1-2, 3); *crassicaudatus* (1-2, 2-3); *cupreus* (1, 2-3); *empetrus* (1, 2-3); *festae* (3, 3; one speci-

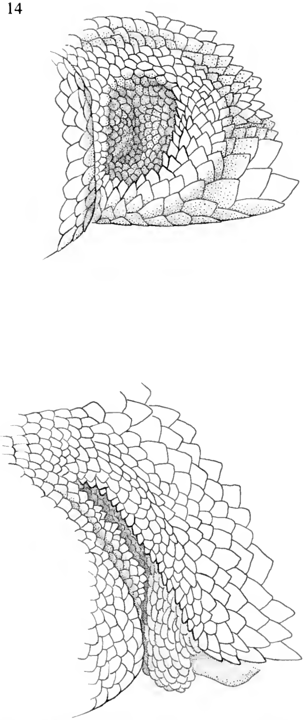

Fig. 2. Dermal mite pockets of *Stenocercus percultus* new species (FMNH 232517, adult male). Top, posthumeral pocket (Type 4). Bottom, postfemoral pocket (Type 5). See also Fig. 3. Anterior to the left. Drawn by L. Meszoly, used with permission of E. E. Williams.

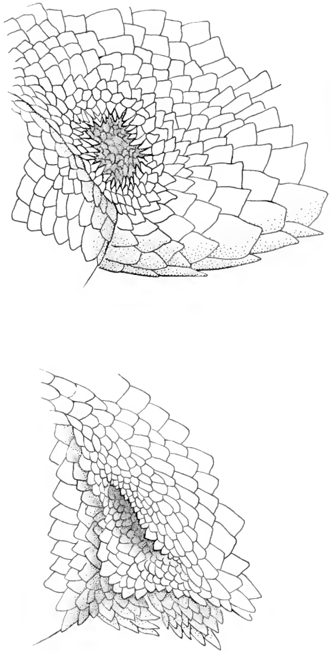

Fig. 3. Dermal mite pockets of *Stenocercus huancabambae* new species (MCZ 18794, adult male; right side, reversed). Top, posthumeral pocket (Type 4). Bottom, postfemoral pocket (Type 5). See also Fig. 2. Anterior to the left. Drawn by L. Meszoly, used with permission of E. E. Williams.

men, CAS 93924, had a much better-developed posthumeral pocket than other *festae* examined, approaching Type 4; this was also the largest specimen, SVL 94); *formosus* (1, 5); *guentheri* (1-2, 1-2; Fritts [1974] notes posthumeral pockets as "absent or . . . weakly developed" and postfemoral pockets as "variable in size" in this species; Castro and Ayala [1982], presumably referring to recently discovered Colombian specimens, note the posthumeral pockets as "little to well-developed"); *humeralis* (1-2, 3); *iridescens* (1-2, 1); *marmoratus* (1, 1); *melanopygus* (1, 3); *moestus* (1, 1); *nigromaculatus* (2-3, 5); *ochoai* (1, 3; Fritts

[1974] reports postfemoral pocket as "deep" in this species; in the only adult male I examined, FMNH 34125, there is a distinct pocket but its depth is about one-half the diameter of the opening); *orientalis* (1, 4-5); *ornatissimus* (1, 1); *ornatus* (4, 5); *praeornatus* (1-2, 5); *rhodomelas* (4, 5); *roseiventris* (1-2, 5); *simonsii* (1, 3); *trachycephalus* (1, 5); *varius* (1, 1-2).

Osteological Characters

Dry skeletal material was available for all of the new species described herein, and several specimens were cleared and double-stained for cartilage and bone using the method of Dingerkus and Uhler (1977). Extensive descriptions or comparisons of osteological characters were not undertaken. However, the conditions of the osteological characters discussed by Etheridge (1966) were determined, and a few of the osteological features discussed by Frost (1988) are noted. The state of the inscriptional ribs (= parasternal ribs of Etheridge 1966) is not easily discernible in dry skeletons, so this feature is reported only for species in which cleared and stained specimens were available. Terminology for the osteological features follows Etheridge (1965, 1966) and Frost (1988). External measurements of specimens prepared for dry skeletons in the field were taken from freshly-killed animals.

Other Features

Coloration in life was derived from detailed notes for particular specimens. Comments on variation were taken from more general descriptions of coloration or from color transparencies.

Comments on reproductive state of females are made only when such observations could be made without destructive dissection (specimens that were skeletonized or had openings in the body wall from tissue sampling or gunshot wounds).

A Note On Localities

The names for localities referred to herein as "Monte Seco" and "Río Zaña" are variously spelled "Monteseco" and "Río Saña" or "Río de Saña," respectively. I use the former spellings because they appear on the 1:100,000 map "Chongoyape" [Departamento Lambayeque; 1977] produced by the Instituto Geográfico Militar (IGM), Lima, which I used for field locations. Other maps produced by IGM use the alternative spellings, and both spellings appear in the literature associated with this area. Regardless of which spelling is chosen, the important point is that the corresponding alternatives refer to the same localities. In the discussion I use "Bosque Monteseco" as a general term to refer to the humid forest located between about 1500m-2500m on the slopes directly above the town of Monte Seco (Dillon and Cadle 1991). For brevity, in the species accounts and discussion I use the terms "Abra de Porculla" and "Canchaque" as collective terms, respectively, for specimens collected just west of the Abra de Porculla (Departamento Piura) at about 2000m, and from about 1740m-1850m on the slope east of the town of Canchaque (Departamento Piura). The precise locality designations for these are given in the lists of specimens examined, and these localities are indicated in Fig. 29.

Reference to the maps will aid in interpreting my discussions of distribution patterns. Figures 4 and 5 show distributions in northern Perú and southern Ecuador of various species of *Stenocercus* discussed herein. Figure 6 shows local place names and topography in the vicinity of Monte Seco, an area of major focus in this study. Figure 29 shows physical features and place names for the area of northern Perú under consideration, and is referred to mainly in the Discussion.

Institutional Abbreviations

AMNH	American Museum of Natural History, New York, NY
ANSP	Academy of Natural Sciences, Philadelphia, PA
BMNH	The Natural History Museum, London (formerly, British Museum of Natural History)
CAS	California Academy of Sciences, San Francisco, CA
CM	Carnegie Museum of Natural History, Pittsburgh, PA
FMNH	Field Museum of Natural History, Chicago, IL

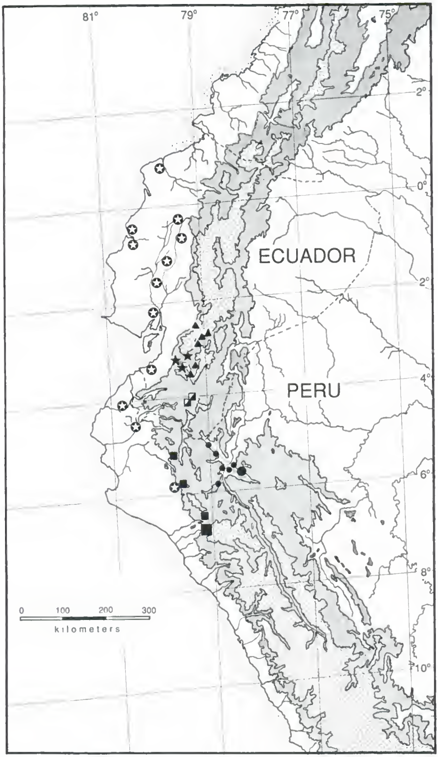

Fig. 4. Map of Ecuador and northern Perú showing distribution of some species of *Stenocercus* discussed in this paper. Shaded area is the Andes; stippled area is above 1000m elevation; hatched area is above 3000m. **Large solid square** denotes type locality for *S. percultus* and *S. imitator*; **Large solid circle** denotes type locality for *S. huancabambae*. *S. percultus* and *S. imitator*, **solid squares**; *imitator* is known only from the two northernmost localities in addition to the type locality. *S. huancabambae*, **solid circles.** *S. iridescens*, **stars within circles.** *S. ornatus*, **half-filled squares.** *S. festae*, **solid triangles.** *S. rhodomelas*, **solid stars.** Localities noted for *iridescens*, *ornatus*, *rhodomelas*, and *festae* are not intended to be comprehensive, but do indicate the approximate limits of their ranges as presently known. For the latter three species, some localities from Fritts (1974) are included in addition to those for specimens examined in this study. The Peruvian records for *iridescens* are the first reported for that country.

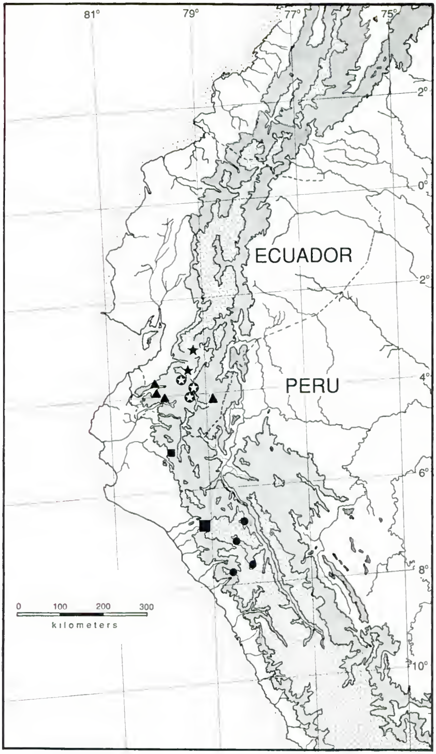

Fig. 5. Map of Ecuador and northern Perú showing distribution of some species of *Stenocercus*. Shaded area is the Andes; stippled area is above 1000m elevation; hatched area is above 3000m. **Large square** denotes the type locality for both *S. eunetopsis* and *S. chlorostictus*; **small solid square** is an additional locality for *S. chlorostictus*. *S. empetrus*, **solid circles**. *S. simonsi*, **solid stars**. *S. humeralis*, **stars within circles**. *S. carrioni*, **solid triangles** (the triangle east of the Andean crest just south of 4° S is Zamora, the type locality for *carrioni*).

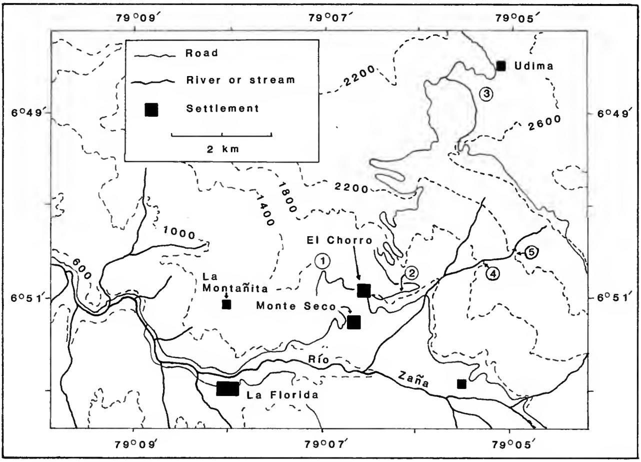

Fig. 6. Map of the Monte Seco region, Río Zaña, Depto. Cajamarca, Perú, showing local place-names and topography. (1), (2), and (3) mark, respectively, the type localities for *Stenocercus percultus* new species, *S. imitator* new species, and *S. eunetopsis* new species; the type locality for *S. chlorostictus* new species, is the village of El Chorro. Localities (4) and (5) are, respectively, Cadle's basecamp at 1800m and Chorro Blanco, a high waterfall and local landmark.

KU	University of Kansas Museum of Natural History, Lawrence, KS
LACM	Natural History Museum of Los Angeles County, Los Angeles, CA
LSUMNS	Louisiana State University Museum of Natural Science, Baton Rouge, LA
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA
MVZ	University of California, Museum of Vertebrate Zoology, Berkeley, CA
SDSU	San Diego State University, Zoology Department, San Diego, CA
UMMZ	University of Michigan Museum of Zoology, Ann Arbor, MI
USNM	National Museum of Natural History, Washington, D. C.

ACCOUNTS OF SPECIES

Stenocercus percultus, new species
Figs. 2, 7

HOLOTYPE.—FMNH 232525 (field number J. E. Cadle 8158), an adult male collected 13 June 1987 from approximately 1-2 km (airline) NNW Monte Seco, along an acequia [irrigation ditch] running between El Chorro and La Montañita, 1350-1380m, Río Zaña, Departamento de Cajamarca, Perú. El Chorro and La Montañita are small settlements approximately 1km N and 3km W, respectively, of Monte Seco (Fig. 6).

PARATYPES (all collected by J. E. Cadle unless otherwise specified).— PERÚ: DEPTO. CAJAMARCA: RIO ZAÑA: Approximately 1km (airline) NE Monte Seco along El Chorro-Monte

Chico Rd., 1330-1370m: FMNH 232515, 232519, 232523 (all adult males), collected 3 June 1987. Approximately 1-2km (airline) NNW Monte Seco along acequia running between El Chorro and La Montañita, 1350-1380m: FMNH 232516 (adult male collected 13 June 1987), FMNH 232626 (adult female collected 13 June 1987); FMNH 232520, 232524 (adult and subadult males, respectively, collected 14 June 1987); FMNH 232530 (adult male, skin and associated skeleton, collected 14 June 1987). 0.5km (airline) SW Monte Seco, 1170m: FMNH 232517 (male), collected 17 June 1987. Approximately 1.5km NE (airline) Monte Seco 1490-1500m: FMNH 232518, 232521, 232527, 232529 (adult males), FMNH 232637 (adult female), collected 17 June 1987. Cerro Condoroáz near quebrada San Isidro, approximately 6km (airline) WSW Monte Seco, 800-1000m: FMNH 232522 (adult male), FMNH 232526 (adult female) collected 6 June 1987 by locals. Trail between Monte Seco and Chorro Blanco approximately 2km (airline) NE Monte Seco 1550-1570m: FMNH 232528 (adult male) collected 12 May 1987. 0.5km by road E El Chorro (=1km NE [airline] Monte Seco), 1450-1500m: FMNH 232531-33 (all adult males, skins and associated skeletons) collected 18 June 1987. 1.5km NE (airline) Monte Seco, 1600m: ANSP 31761 (hatchling) collected 18 January 1989. Monte Seco-Udima Road, 0.5km E El Chorro, 1450m: ANSP 31762-63 (adult females) collected 20 January 1989.

PERU: DEPTO. CAJAMARCA: Llama [on the Río Maichil, a tributary of the Río Reque; 2095m, fide Stephens and Traylor 1983]: MCZ 121234, collector and date unknown.

PERU: DEPTO. PIURA: 2km W Porculla Pass (30km ENE Olmos), 6500ft. [1982m] [Note: given erroneously as Depto. Lambayeque on specimen tags, but corrected in the specimen catalogue of C. B. Koford for his field numbers 4068-74]: MVZ 82318-20 (subadults), 82365-68 (adult males), 119223-24 (adult females), 119225-29 (adult males), 119230-31 (adult females), collected 17, 18, and 31 August 1967 by R. Hilborn, R. B. Huey, and C. B. Koford. About 15km (by road) E Canchaque on Huancabamba road, about 5700ft. [1738m]: SDSU 1596 (adult male), LSUMNS 27224-29 (adult females and subadults), collected 9-10 December 1974 by Richard Thomas.

DISTRIBUTION (Fig. 4).— *Stenocercus percultus* is known from the Pacific slopes of the Andes in the upper Río Zaña (800-1600m elevation) and upper Río Reque (2095m elevation), Depto. Cajamarca, Perú; from west of the continental divide near the Abra de Porculla, Depto. Piura, Perú (1990m elevation); and from near Canchaque, Depto. Piura, Perú (1738m elevation). Although *S. percultus* is not known east of the continental divide, it occurs very near the summit of the Abra de Porculla, the low pass separating the Pacific versant from western tributaries of the Río Marañon drainage, and might also be expected in the upper reaches of inter-Andean valleys of the Huancabamba Deflection (see comments under Distribution in the account for *S. huancabambae*).

ETYMOLOGY.— The specific epithet, *percultus*, is a Latin adjective derived from the prefix "*per-*," meaning "very" or "highly," and the adjective "*excultus*," meaning "adorned" or "elegant;" hence, "highly adorned," in reference to the beautiful and very colorful males of this species.

DATA ON THE HOLOTYPE.— Snout-vent length, 99. Tail length, 223. Total length, 322. Scale rows around midbody, 50. Scales across the gular region, 23. Internasals, 4. Supraoculars, 5. Subdigital lamellae on the 4th finger and toe, 19 and 29, respectively.

CHARACTERIZATION.— *Stenocercus percultus* may be characterized by the following combination of features: (1) head scales keeled, multicarinate, or wrinkled; (2) no distinct parietal, interparietal, or postparietal scales; posterior head scales small, irregular, juxtaposed; (3) internasals 4, occasionally 3 or 5; (4) no enlarged, or only slightly enlarged, supraocular row; (5) two canthals on either side between the superciliaries and the small postnasals or nasal; (6) no projecting blade-like angulate temporals; (7) gulars generally smooth; (8) parietal eye not distinct, sometimes not visible; (9) a prominent, but short, gular fold; other neck folds generally weakly developed; (10) paradorsal scales large, imbricate, mucronate, and strongly keeled; (11) prominent serrate vertebral crest in adult males; weak in females; (12) deep posthumeral and postfemoral pockets; Types 4 and 5, respectively (Fig. 2); (13) scales of posterior thigh small, imbricate, keeled; (14) tail moderately

compressed, not distinctly higher posterior to the pelvis than at pelvis; (15) sexes strongly dimorphic in coloration and pattern, but a light facial mask in loreal/upper labial region is present in both; adult males generally with chin and medial throat region entirely black; dorsum brownish with darker bars or chevrons, more distinct in females and subadults than in adult males; venter of adult males reddish, usually without extensive black pigment (confined to narrow midventral strip if present).

DIAGNOSIS.—*Stenocercus percultus* differs from all species of *Ophryoessoides* sensu Fritts (1974) in lacking enlarged posterior head scales and keeled ventral scales, and in having a relatively more rounded tail. It can be distinguished from all other species of *Stenocercus* by having the combination of (1) deep posthumeral and postfemoral pockets (Types 4 and 5, respectively); (2) juxtaposed, protuberant, wrinkled or multicarinate dorsal head scales; (3) four internasal scales (occasionally 3 or 5); (4) weakly-developed and incomplete series of neck folds; and (5) keeled, imbricate scales on the posterior surface of the thigh.

DESCRIPTION.—*Head* (Fig. 7). Dorsal head scales small, juxtaposed, and keeled, multicarinate, or wrinkled (keels tend to be weak in the antorbital region of small females). Parietal region broken up into many small scales which, particularly in large males, are protuberant. Rostral large, with projecting tip dorsomedially; in contact with the first supralabials, the first lorilabials, and medially with either two or three (rarely four) postrostrals. Medial postrostrals much broader than long if only 2 present or, if 3, one is much smaller than the other two, which are broader than long. Nasal separated from first labial by the first lorilabial. Two canthals in front of superciliary series, the anterior one usually in contact with the nasals, rarely separated from it by tiny scales. Generally four elongate superciliaries overlapping posteriorly, followed by two shorter posterior superciliaries overlapping in the reverse direction. Internasals generally 4 (rarely 3), the medial pair much broader posteriorly than anteriorly; occasionally one or more of the internasals is divided horizontally. No enlarged supraoculars, or if one row appears enlarged, its largest scale is usually less than twice the size of scales in adjacent rows of supraoculars. Supraoculars wrinkled or tuberculate, sometimes distinctly keeled. No distinct parietal, interparietal, or postparietal scales. The parietal eye is visible in slightly more than one-half (56%) of the specimens, and may be visible or not in males, females, or subadults; a greater proportion of individuals from northern populations (Abra de Porculla and Canchaque) lack visible parietal eyes than those from the Río Zaña. Lateral temporal scales slightly imbricate and weakly keeled. Border between lateral temporal scales and posterior dorsal head scales is marked by one or two elongate, strongly keeled scales. A few gular scales between anteriormost postmentals sometimes appear pointed or weakly keeled; otherwise all gulars are smooth. Mental in contact with the first infralabials and the first pair of postmentals, which are followed by a series of three (rarely four) enlarged postmentals on each side. First postmentals in contact medially, and with the first infralabial and (usually) the first sublabial on each side.

Neck and body. Dorsal and lateral neck and body scales large, imbricate, mucronate, and strongly keeled except posterior to ear, where they are somewhat smaller and moderately keeled. Preauricular fringe well-developed. Adult males have a prominent, projecting, serrate vertebral crest extending from the nape onto the base of the tail; from this point it gradually decreases in size and disappears 1/2 - 2/3 the length of the tail. Females and subadult males have a weakly projecting vertebral crest. Paradorsal and lateral scales mucronate and strongly keeled. Ventral body scales smooth. Ventral scales equal to or slightly smaller than dorsal scales.

Neck folds. Skin of neck region in general not prominently folded. Dorsolateral and antehumeral folds weakly-developed. Prominent, but short, gular fold present, not or barely extending onto ventral surface of pectoral region. Supra-auricular fold usually very weakly-

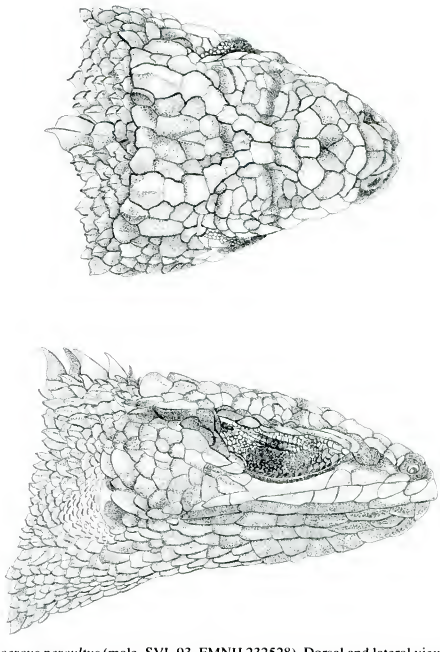

Fig. 7. *Stenocercus percultus* (male, SVL 93, FMNH 232528). Dorsal and lateral views of head. Perú: Depto. Cajamarca: Río Zaña, trail between Monte Seco and Chorro Blanco approximately 2 km (airline) NE Monte Seco, 1550-1570m. Drawn by G. Bisbee.

developed. Sometimes (especially large males) a weak oblique neck fold is present. No postauricular, rictal, or longitudinal neck folds. Antegular fold sometimes evident as a slight groove posteroventrally to ear.

Tail. Dorsal and ventral scales of the tail are unicarinate and mucronate except for a postanal series. Tail moderately to strongly compressed.

Limbs. Dorsal and ventral scales of forelimbs keeled; on the hindlimbs, the dorsal scales are keeled, the ventral ones smooth. Scales on posterior surfaces of thighs small, imbricate, and keeled. Supradigitals of forelimbs smooth, of hindlimbs strongly unicarinate. All subdigitals multicarinate. Plantar scales strongly unicarinate; palmar scales strongly unicarinate, occasionally multicarinate.

Dermal Pockets (Fig. 2). Posthumeral and postfemoral pockets of types 4 and 5, respectively, but subject to some geographic variation (see below). The following descriptions are

based on individuals from the Río Zaña.

The posthumeral pocket is a deep cavity in the axilla, bordered posteriorly and dorsally by a raised, thickened fold of skin, which is covered by tiny imbricate scales. Its opening is rounded or an open arc depending on the position of preservation. The lining of the pocket itself is composed of a deep loose skin pouch covered with small pointed scales peripherally, more granular scales deeply. There is a thickened patch of skin devoid of scales on the anterior wall of the pocket. The pocket of females is only half the depth that of males. Among males, there is also variation in posthumeral pocket depth, but this does not appear strongly correlated with body size.

The opening of the postfemoral pockets is an oblique slit immediately behind the limb insertions, from which the pocket extends posterodorsally. The opening is much more than half the height of the thigh. The pouch is lined by pointed scales toward the periphery and granular, pavement-like scales deep in the pouch. The depth of the pouch is approximately equivalent to 9-10 scale rows on its outside wall.

Pattern. Dorsum generally brownish with darker brown crossbars or chevrons (obscure in adult males, obvious in females and subadults). A distinctive whitish or grayish loreal/subocular mask in both sexes (Fig. 7). Mental and gular regions of adult males black midventrally, lighter laterally; pectoral region of adult males with blackish patch anteriorly, followed by light bar, another dark bar, and a light bar before grading into belly coloration. Females have a dorsolateral light stripe from the temporal region to the tail (fading posteriorly), conspicuous dark dorsal bars or chevrons, and a grayish venter heavily speckled with darker brown. See Coloration for details.

Scale counts and measurements (Tables 1 and 2). Body scales moderately large. Vertebral (dorsal crest) scales are very large, resulting in relatively low meristic values. The tail is much more than twice the body length.

Size and sexual maturity. The largest male (FMNH 232523) has a SVL of 105 (another male, FMNH 232530, had a SVL of 107 when measured freshly-killed before skeletonization); the largest female (FMNH 232526) has a SVL of 86. The smallest males showing indications of adult coloration (see below) are MVZ 82366 and 82368 (SVLs 54 and 57, respectively). These individuals show indications of such adult features as the concentration of dark pigment midventrally in the gular region and the light patches in the pectoral region. The smallest adult female (MVZ 119224; gravid) has a SVL of 60.

Geographic Variation and Sexual Dimorphism. Geographic and sexual variation for meristic characters and body size in *Stenocercus percultus* is summarized in Table 2. Sexes do not differ significantly in meristic data within either the Río Zaña or the Abra de Porculla populations. With the small population samples available the only significant difference among populations is the mean value for midbody scales between females of the Río Zaña and the Canchaque populations (note that the range for this variable in the Canchaque population is encompassed by that in the Porculla population). There is a weak tendency, however, for the more northern populations (Depto. Piura) to have somewhat higher overall meristic values than the southern samples (Depto. Cajamarca).

The sexes are strongly dimorphic in coloration and pattern (see below: Coloration). There are no obvious and consistent qualitative differences in coloration or pattern between the Abra de Porculla and the Río Zaña populations. In the sample from the Río Zaña thirteen of twenty specimens have SVLs >90, whereas none of the sixteen Porculla specimens are of this size; this may indicate body size differences between the two populations.

The seven specimens from near Canchaque, Depto. Piura comprise three adult females (LSUMNS 27224, 27226-27), three subadults (LSUMNS 27225, 27228-29), and one adult male (SDSU 1596), and they have meristic values similar to specimens from the other populations (Table 2). Females and subadults differ, however, in several qualitative respects from specimens from the two other known

Table 2. Geographic and Sexual variation for meristic counts and body size among populations of *Stenocercus percultus*. For meristic characters, range (sample size), and mean ± S.D. are given for each sex. Populations are indicated in Fig. 1.

		Depto. Cajamarca		Depto. Piura	
	Sex	Río Zaña	Llama	Porculla	Canchaque
Midbody scales	M	50-62 (14) 55.93 ± 2.99	55 (1)	53-65 (9) 58.67 ± 3.35	61 (1)
	F	50-55 (5) 52.0 ± 2.0	—	53-61 (5) 55.40 ± 3.51	56-61 (3) 58.33 ± 2.52
Vertebral scales	M	35-46 (14) 40.57 ± 2.87	45 (1)	40-43 (8) 41.25 ± 1.28	40 (1)
	F	39-48 (5) 42.8 ± 3.70	—	36-46 (5) 41.80 ± 3.63	45-47 (3) 46.0 ± 1.0
Paravertebral scales	M	67-77 (14) 71.0 ± 2.75	70 (1)	65-77 (8) 72.25 ± 4.62	73 (1)
	F	62-69 (5) 66.2 ± 3.03	—	66-73 (5) 69.40 ± 2.70	65-74 (3) 69.0 ± 4.58
Gular scales	M	23-27 (14) 24.14 ± 1.46	25 (1)	23-27 (8) 25.50 ± 1.69	27 (1)
	F	21-24 (5) 22.80 ± 1.30	—	23-27 (8) 23.6 ± 2.07	22-25 (3) 23.33 ± 1.53
Lamellae, 4th finger	M	17-22 (14) 20.21 ± 1.37	22 (1)	17-22 (9) 19.67 ± 1.73	20 (1)
	F	17-21 (5) 19.60 ± 1.67	—	17-19 (5) 18.20 ± 0.84	17-20 (3) 18.33 ± 1.53
Lamellae, 4th toe	M	26-32 (13) 28.54 ± 1.90	29 (1)	24-31 (9) 27.33 ± 2.45	28 (1)
	F	26-28 (5) 27.2 ± 0.84	—	26-29 (5) 27.40 ± 1.14	24-26 (3) 25.0 ± 1.0
Snout-Vent Length (mm)	M	67-105 (14)	65 (1)	54-85 (9)	89 (1)
	F	62-86 (5)	—	60-71 (5)	69-80 (3)

general localities, and the following comments characterize the similarities and differences in these features. In addition to quantitative scale count similarities, the Canchaque specimens are similar to other *S. percultus* females and subadults in having (1) a thin light antehumeral bar; (2) a light lorilabial mask, sometimes continuous with a light temporal stripe and dorsolateral light stripe; (3) a similar head scale pattern, including one row of slightly enlarged supraoculars; (4) head scales juxtaposed and wrinkled, but distinctly keeled only on the outer scales in the parietal region; and (5) similar pigment patterns in the pectoral region consisting of light and dark mottling or vermiculations.

Females and subadults from Canchaque differ from other *S. percultus* females as follows: (1) they have consistently dark throats, bluish (in preservative) in LSUMNS 27224, 27229 (some *percultus* females from other populations have a tendency toward dark throat patterns, but not so extensive as in the Canchaque series, and never bluish in the specimens examined). (2) The lateral neck scales are smaller and less mucronate in the Canchaque series than in other *percultus* specimens. (3) Only two of the Canchaque specimens (LSUMNS 27228-29) have the normal pattern of four internasal scales for *percultus*; the others have 2-3 internasals that are very irregular in shape. (4) The Canchaque specimens have a very small posthumeral pocket, only slightly indicated as a depressed area containing very small flat scales in the axillary region. In other *percultus* females there is generally a distinct pocket with a thickened, raised rim surrounding it. However, MVZ 119231 from the Abra de Porculla is similar to the Canchaque individuals in having only a slight depression. In general, specimens from the Abra de Porculla and the single specimen from Llama, Cajamarca (MCZ 121234) have less well-developed posthumeral pockets than those of topotypes. This may simply be a reflection that all individuals from the former localities are smaller than males available in the sample from the Río Zaña.

COLORATION.— *Coloration in Life. Adult males.* (based on detailed notes for FMNH 232528; SVL 93).— Dorsal ground color of the body and tail light yellowish brown. Scales forming the dorsal crest mostly brown of a slightly darker shade than the dorsal ground color; about every third or fourth scale of the crest is yellow. There is a vague indication of darker brown crossbands on the dorsum, beginning middorsally with scales forming the dorsal crest, but these are very faint. Head brown with some black and yellow spots. A black canthal stripe continues onto the lower eyelid, where it widens to form a blackish mask. Upper eyelid and posterior part of the lower eyelid yellow. A pale yellow line extends from behind the eye to above the tympanum and is bordered below by a black line. Upper labials pale yellow bordered below by black. Lower labials, postmentals, mental, and medial part of gular and throat regions black (wider anteriorly, narrower posteriorly). This black pigment is confluent with a black patch in the anterior pectoral region at the level of the gular folds, and a transverse black bar extends across the pectoral region at this level. The lateral throat and gular regions between the black patches is bright red, and this extends dorsally to the level of the lower labials and lower edge of the tympanum. Some red pigment visible within the black patch of the anterior pectoral region, as if black pigment is on top of the red pigment. A pale yellow pectoral bar is bordered posteriorly by a black bar, which is in turn bordered posteriorly with a triangular pale yellow patch on the midline and a few yellow scales more laterally. Scales of the anterior belly region reddish tipped with black; those of the anterior half of the belly behind these bright lavender tipped with red. Those of the posterior half of the belly light brown tipped with medium brown. A black triangular patch present just anterior to the hind limbs, extending posteriorly across the pelvic region.

Ventral surface of the tail dirty yellow for about six scale rows behind the vent, followed by lavender which grades imperceptibly into a medium dull brown. Ventral surface of limbs brown with mottling of yellow and reddish

brown. Upper surface of limbs yellowish brown as in the dorsal ground color. Right lateral surface of the body bright red with yellow flecks which cover single scales; left lateral surface similar but reddish brown rather than bright red.

Variation in males.— Extent of black pigment on the chin, throat, and belly of adult males variable. In three individuals (FMNH 232515, 232522, 232529), the black on the chin and throat is extensive, covering most of the ventral surface of the head anterior to the pectoral region; in these the black is densest toward the midline and some red is still evident on the lateroventral part of the throat. The only specimen with a continuous black ventral stripe, SDSU 1596, has a narrow midventral stripe extending from the pectoral to the pelvic region. The number of yellow scales in the dorsal crest varies from many (nearly every scale with some yellow) to few.

Adult females (based on FMNH 232526; SVL 86).— Middorsal area of body medium brown with darker brown triangular or chevron-shaped blotches (four blotches between the forelimb and hindlimb insertions). Dorsal surface of head medium brown with dark brown to black irregular splotches. Upper and lower labials very dark brown. A dull yellow vertical bar extends from below the posterior part of the eye and meets a bright yellow loreal bar extending from the rostrum and occupying the loreal region and scales between the eye and upper labials. A yellow stripe extending from the postorbital vertical bar passes above the tympanum and dorsolaterally along the body. Posterior to the tympanum this stripe fades to a yellowish brown and broadens posterior to the forelimbs (the broadening is not due to the stripe covering more scale rows, but the fact that the scales become larger on the lateral surface of the body). Lateral surfaces of body brown to yellowish brown. Dorsal surface of limbs medium brown, barred obscurely with dark brown. Dorsum of feet greenish yellow with darker markings. Ventral scales of throat, pectoral region, belly, and thighs yellowish edged with bright red (giving a rosy appearance when not viewed closely). The red is denser on the throat and on the pelvic scales. A triangular area of dark brown scales is present in the gular region. Ventral scales of the forelimbs and shank mottled yellowish, greenish yellow, and brown, and many are also red-tipped. Ventral base of tail colored as the belly (the distal portion of the tail is regenerated).

Subadult males (based on FMNH 232524; SVL 67).— Specimen is similar to adult males except in the following features: (1) Dorsum obscurely barred with yellow and dark brown irregular chevrons (apex posteriorly). (2) Black on the chin and throat not as extensive, this area being mostly red. (3) There is more extensive palė yellow pigment in the pectoral region. (4) The red on the flanks restricted to the axillary and groin regions. In its place the flanks are medium brown flecked with yellow. (5) There is very little lavender pigment ventrally, and it is restricted to the area just posterior to the pectoral region. Individual scales of the abdominal region are tan outlined with medium brown. (6) Ventral base of the tail bright yellow.

Distinctive pattern features of S. percultus.— A distinctive feature of both males and females of *S. percultus* is a light (white, dusky white, or yellowish in life) loreal-subocular mask (Fig. 7). In females this continues as a dorsolateral light stripe on the anterior trunk. This mask is evident in hatchlings (ANSP 31761) and allows easy field identification of hatchlings, juveniles, and females of this species from those of the sympatric species, *Stenocercus imitator* new species, which otherwise are patterned similarly.

Coloration in preservative.—In adult males, dorsum brown with a few darker irregular bars in some individuals, and scattered grayish flecking (probably corresponding to the red color in life). There is general fading of all bright colors. The red pigment on the throat and belly is persistent, being faded red in the 1987 sample from the Río Zaña, and pinkish in the Abra de Porculla sample (MVZ) collected in 1967. All other light ventral colors of males (yellow, lavender) fade entirely, as does the red pigment on the dorsum, leaving the corre-

sponding scales grayish white or brown depending on the underlying pigment. The dorsum of one subadult male (FMNH 232524) retains a series of middorsal dark brown chevrons, each bordered posteriorly by a light grayish-brown chevron. The dorsal chevrons of this specimen are not as bold as those of three adult females (FMNH 232526, 232626, 232637).

Females turn brown to grayish brown in preservative, with retention of darker middorsal pattern and light dorsolateral stripes. Ventrally they are grayish white to yellowish gray with darker speckling and reticulations.

COMPARISONS.— *Stenocercus percultus* is similar to *S. huancabambae* new species, described below. Given their geographic proximity (Fig. 4) they may eventually be found sympatrically in the upper Río Chamaya or Río Huancabamba valleys. *Stenocercus percultus* may be distinguished from *S. huancabambae* (characters in parentheses; see Figs. 7-9 and Table 1) by the following features: (1) smaller body scales, 52-65 around midbody and 62-77 paravertebral scales (larger, 37-52 at midbody and 48-64 paravertebrals); (2) dorsal body scales strongly keeled (weakly to moderately keeled); (3) 4, rarely 3, internasals (6, occasionally 5, rarely 4 or 7); (4) posterior head scales small, highly rugose, and protuberant in adult males, and without distinct parietals, interparietal, or postparietals (larger, juxtaposed, and not rugose or protuberant; distinct parietals, interparietal, and postparietals); (5) no projecting angulate temporals (2); (6) parietal eye indistinct or absent (consistently distinct); (7) no distinctly enlarged row of supraoculars (one row of enlarged supraoculars); (8) smooth ventrals (keeled); (9) antehumeral fold and weak neck fold present (both absent); (10) tail moderately compressed in adult males, gradually decreasing in height posteriorly from the vent (very strongly compressed in large adult males, first increasing in height posteriorly from the vent, then gradually decreasing); (11) chin and throat of adult males usually with much heavy black pigment concentrated toward the midline (mostly without dark pigment; occasionally a dark brown midventral spot or vague streaking); (12) ventral color of adult males with deep red pigment and a midventral dark stripe (pink, usually without dark pigment); (13) no dark scapular spot (present).

Stenocercus percultus may be distinguished from *S.* (*Ophryoessoides* sensu Fritts 1974) *iridescens*, a species of western Ecuador and northwestern Peru (Fig. 4), by the following features (*iridescens* characters in parentheses; see Figs. 7 and 10): (1) dorsal head scales keeled (smooth); (2) no greatly enlarged supraoculars (one row of greatly enlarged supraoculars); (3) internasals 4, rarely 3 (2, occasionally 3); (4) posterior head scales small, protuberant in large males (large, flat even in large individuals); (5) no distinct parietals, interparietal, or postparietal (all distinct); (6) parietal eye indistinct or absent (always distinct); (7) antehumeral and weak neck folds present (absent); (8) posthumeral and postfemoral pockets deep (shallow and absent, respectively); (9) chin and throat of adult males usually with heavy black pigment concentrated toward the midline (lacking; black flecking posterolaterally on throat). No other species of *Ophryoessoides* (sensu Fritts 1974) are presently described from west of the Andes in Ecuador or Perú.

Fritts (1974) recorded 17 species of *Stenocercus* sensu stricto from western Perú and Ecuador or inter-Andean valleys of northern Perú and southern Ecuador. *Stenocercus percultus* can generally be distinguished from these by its relatively large size, moderately large dorsal body scales, compressed tail, high dorsal crest, and distinctive color pattern (see description). It differs from 13 of the species (*carrioni*, *chrysopygus*, *empetrus*, *guentheri*, *haenschi*, *humeralis*, *ivitus*, *melanopygus*, *moestus*, *nigromaculatus*, *nubicola*, *ornatissimus*, *varius*) in having a deep (type 4) posthumeral pocket (absent to weakly developed [types 1-2] in these species of *Stenocercus*; see Materials and Methods, and Fritts [1974]). The presence of a projecting vertebral crest will also distinguish *Stenocercus percultus* from all of these except *S. nigromaculatus* and *S. nubicola*, which also have projecting crests (a strongly keeled, but not projecting, vertebral row

is present in *S. varius* and *S. humeralis*). *S. percultus* differs from *S. festae* in having a somewhat more well-developed antehumeral fold (weakly evident in some *festae*, not clearly "absent," as reported by Fritts 1974), much more well-developed posthumeral and postfemoral pockets (types 4 and 5, respectively, in contrast to types 3 and 3 in *festae*), and in lacking extensive black pigment on the venter of adult males. It differs from *S. simonsi* in lacking enlarged spinose caudal scales, in having fewer midbody scales (73-102 in *simonsi*; Fritts 1974 and below), and in having deep (type 4) posthumeral pockets (type 1 in *simonsi*). An amended description of *S. simonsi* is provided below.

Two other species of *Stenocercus* from southwestern Ecuador, *S. rhodomelas* and *S. ornatus*, have deep posthumeral pockets (type 4) and projecting vertebral crests. *Stenocercus percultus* can be distinguished from these species as follows (*S. percultus* characters in parentheses). *Stenocercus rhodomelas* has smooth or only vaguely keeled anterior dorsal head scales (usually obviously carinate; occasionally only weakly so); juxtaposed, weakly keeled posterior head scales which are not, or only weakly, protuberant (strongly protuberant in adult males, multicarinate); no gular fold or a very weak one (well-developed, although short); somewhat fewer midbody and gular scales, 46-56 and 18-23, respectively (Fritts, 1974) (51-65 and 20-28, respectively); and generally 2, occasionally 3, internasals (usually 4). In addition, the patterns of adult males differ in the two species. In *S. rhodomelas* the dorsum is brown in preservative, usually with distinct black irregular crossbars or chevrons middorsally (no distinct crossbars); a distinct black blotch anterodorsal to the forelimb insertions (absent); throat with extensive black pigment not concentrated toward the midline (black concentrated toward the midline); venter with extensive black pigment midventrally from the pectoral to the pelvic region, and on the ventral surfaces of the thighs and shank (no extensive black on venter; none on ventral surfaces of hind limbs; however, see comments on the Porculla population). Adults of *S. rhodomelas* have 1-2 rows of light sublabial scales medial to the infralabials, with a sharp border delimiting the light area from the black infralabials and gulars (all sublabials black or dark-colored in adults).

Stenocercus ornatus can be distinguished from *percultus* (characteristics in parentheses) by the following: In *ornatus* the posterior head scales are slightly imbricate and with a distinct central keel [See Boulenger (1885, Plate XII) for figures of the dorsal head scales and general body form of *S. ornatus*] (juxtaposed, protuberant, wrinkled or multicarinate). *Stenocercus ornatus* has somewhat fewer midbody scales, 47-58 (Fritts 1974) (50-65; = 56.6); fewer paravertebral scale rows, 53-59 (N = 5) (62-77); and fewer subdigital lamellae on the fourth finger and toe, 20-24 and 30-35, respectively (N = 5) (17-22 and 24-32, respectively; = 19.6 and 27.5, respectively). *S. ornatus* has prominent supra-auricular and dorsolateral folds, especially in males (these folds only weakly developed). The dorsal color of many preserved individuals of *ornatus* has a coppery tone (plain brown). Adult males of *S. ornatus* have a broad black antehumeral bar extending across the scapular region and sometimes extending ventrally to the lateral part of the pectoral region as well (absent); generally lack black pigment on the throat (present, concentrated midventrally); do not have black pigment continuously across the gular region just in front of the pectoral region (present, and continuous across venter); have two broad bold black bars on each side of the midventral line between the pectoral and pelvic regions, occasionally meeting midventrally to form a single broad midventral stripe that occupies 1/3 or more of the width of the venter (lacks extensive black pigment on venter); and usually have dark gray to black pigment on ventral surfaces of thighs and base of tail (lacking or poorly developed).

Females of *percultus* are the most difficult specimens to distinguish from females of other species of *Stenocercus* occurring in northern Perú and southern Ecuador. The following are

characteristics useful in making these distinctions (characteristics of *percultus* females in parentheses). *S. carrioni* and *S. simonsi* have strongly spinose tails and are not strongly sexually dimorphic (tails not spinose; males and females strongly dimorphic); *S. ivitus* and *S. nubicola* females have granular posterior thigh scales (imbricate); *S. humeralis* has granular scales posterior to the tympanum and on the lateral surface of the body (imbricate in each case); in *S. guentheri* the lateral neck scales posterior to the tympanum are about the same size as the dorsal neck scales, and many of the dorsal head scales and supraoculars are distinctly keeled (lateral neck scales distinctly smaller than dorsal neck scales, dorsal head scales and supraoculars at most indistinctly keeled); in *S. ornatus* the head scales are strongly wrinkled or keeled (smooth or weakly wrinkled), and the lateral neck scales strongly mucronate and 1/2 or more the size of the dorsal neck scales (weakly mucronate and much smaller than 1/2 the size of the dorsal neck scales; in *S. festae* and *S. rhodomelas* the lateral neck scales are strongly mucronate and about the same size as the dorsal neck scales (weakly mucronate and smaller than 1/2 the size of the dorsal neck scales); *S. festae* differs, in addition, in that the head scales are strongly wrinkled or keeled (smooth or weakly wrinkled); *S. rhodomelas* differs, in addition, in that the throat bears longitudinal dark streaks (without streaks).

OSTEOLOGY.— Dry skeletons of four males were available: FMNH 232530 (SVL 107), FMNH 232531 (SVL 88), FMNH 232533 (SVL 103), and FMNH 232532 (SVL unknown; skull size intermediate between 232531 and 232533). The eight osteological features of Etheridge (1966) which are easily determined in dry skeletons conform to the South American pattern in *S. percultus*. The region of the nasal/frontal contact is well ossified. The parietal foramen is persistent in all but one specimen (FMNH 232533). The superior fossa of the quadrate is variably enlarged (FMNH 232530, 232532) or not (FMNH 232533). The tricuspid maxillary teeth are slightly compressed, unflared, and with blunt cusps. There is variability in the presence of pterygoid teeth. Three specimens (FMNH 232531-33) bear three to four multicuspate teeth on the posteromedial edge of each pterygoid. FMNH 232530 lacks pterygoid teeth altogether, and the posteromedial edge of the pterygoid is smooth.

There is much sculpturing on the dermal roofing bones, especially concentrated on the parietal, frontals, prefontal, postorbital, the posterior half of the nasals, and along the canthal ridge. The sculpturing produces large rugosities, each composed of numerous smaller tuberosities. The rugosities are especially concentrated in the interorbital and posterior skull regions, and are more extensive in larger individuals, in which the parietal and posterior portion of the frontals are extensively sculptured. Similar sculpturing is found in various iguanids (see Etheridge and de Queiroz 1988:291). Although there appears to be a general correspondence between the sculpturing and the overlying scale pattern in *Stenocercus percultus*, the rugosities in general are not as discrete as those illustrated by Etheridge and de Queiroz (1988:290) for *Laemanctus serratus*. In *S. percultus* the borders between rugosities are poorly delimited, which may be partly a reflection of the complex and strongly protuberant head scales in this species.

NATURAL HISTORY OBSERVATIONS.— Most specimens of *Stenocercus percultus* from the type locality were collected from cultivated land or second growth forest. A few were collected from dry scrub forest that characterizes elevations between 800-1000m in the vicinity of Monte Seco. The species was not observed in the humid forest that covers the slopes above Monte Seco above about 1500m; however, because *S. percultus* is very wary and less common than other species of *Stenocercus* in the area, it may eventually be found there. The lower elevational extent of *Stenocercus percultus* in the Río Zaña valley is not known, but it is presently known from one locality at 800-1000m. This species may be an inhabitant of the dry thorn forest that forms a broad transition zone with lower, more xeric habitats between about 600m and 1000m (Koepcke

1961, Weberbauer 1936).

The habitat west of Abra de Porculla (Depto. Piura), where the series of *Stenocercus percultus* in MVZ was collected, is presently somewhat arid (Stephens and Traylor 1983), although some relict humid forest patches were, until recently at least, found in this region (Koepcke 1961). Field notes of R. B. Huey (in MVZ) for 17 and 31 August 1967, when the series was collected, describe the habitat as a "30° slope of a canyon with low brush (3 feet) mixed with large fragmented boulders." Charred tree stumps (R. B. Huey, field notes) at the site suggested that it was previously forested. Several of the MVZ series were taken in a "boulder and plant jumble" on a slope (field notes of C. B. Koford in MVZ). At the type locality, the Abra de Porculla, and in the vicinity of Canchaque, *Stenocercus percultus* is sympatric with *S. imitator* new species. At the type locality and the vicinity of Canchaque it is also sympatric with *S. chlorostictus* new species. Just west of the Abra de Porculla, and probably also in the vicinity of Canchaque, *S. percultus* is parapatric with *S. iridescens* (see Appendix and Fig. 4).

Stenocercus percultus is very wary when active. Most specimens from near the type locality were collected from mid-morning to mid-afternoon on days of full sun. No specimens were collected from beneath surface objects, so this species very likely uses underground retreats or retreats under large surface objects. Most specimens were observed on the ground. However, one large male (FMNH 232626) was sunning on a large log 0.5m from the ground (a female, FMNH 232516, was in leaf litter under a shrub nearby); another male was sunning on top of a large rock 1m in diameter, and two others were collected from 1.5m up on a rock wall along a road cut; a female (FMNH 232637) was collected at the entrance to a hole in a rock wall 1m off the ground. These observations indicate that *Stenocercus percultus* is a least sometimes scansorial and saxicolous. Field notes of R. B. Huey indicate that at the site near the Abra de Porculla, these lizards sought refuge under rocks, boulders, and in the shade of brush.

Females with enlarged ova were collected 6, 13, and 17 June 1987 from the Río Zaña population (FMNH 232526, 232626, 232637), and 18 August 1969 from the Abra de Porculla population (MVZ 119223-24, 119230-31). Body sizes of these females ranged from 60-86mm SVL. Two individuals with SVLs greater than 60mm (ANSP 31762-63) collected in January 1989 from the Río Zaña population, and three adult females (LSUMNS 27224, 27226-27) from the Canchaque population collected in December 1974, had no enlarged ova, as did one female (MVZ 82320) collected 31 August 1967 from the Abra de Porculla population. These observations suggest oviposition during the dry season, but small samples sizes for females collected during the rainy season do not preclude a much more extensive period (see comments on hatchlings below). Clutch sizes for two of the above females (FMNH 232526, SVL 86mm; FMNH 232626, SVL 73 mm) were two eggs each. These clutch sizes, if they prove to be typical, are small for lizards of this body size (compare *S. imitator* new species below).

Two specimens from 2km W Abra de Porculla (Depto. Piura, Perú; MVZ 82318-19; SVL 33 and 36, respectively) and one from the Río Zaña (Depto. Cajamarca; ANSP 31761; SVL 31) are thought to be close to hatching size. The Abra de Porculla specimens were collected 17 and 31 August, corresponding to the middle of the dry season, whereas the Río Zaña specimen was collected 18 January, the beginning of the rainy season. The disparity in hatching dates implied between the two localities suggests different timing of reproduction in these populations, but it is also consistent with an extended or multimodal reproductive period at either locality.

***Stenocercus huancabambae*, new species**
Figs. 3, 8-9

HOLOTYPE.— MCZ 165319, an adult male, one of a series collected 3 November 1982 by P. Hocking, from San José (Bagua Grande), Depto. Amazonas, Perú. According to Stephens and Traylor (1983), this San José is "Across Río Utcubamba on mountain slope facing Bagua Grande" (see Fig. 4).

PARATYPES.— (Note: Because many of the paratypes are subadults and hatchlings, sexes are given only for specimens with SVL > 60). PERU: DEPTO. CAJAMARCA: Bellavista: AMNH 28529-30; MCZ 18791-93 (adult males), 18795, 60030-31, 60033-37, 60040 (adult female), 60042-54; UMMZ 59031 (adult male and female, two subadults), collected in September 1916 by G. K. Noble and the Harvard Peruvian Expedition. 5km W Bellavista: LSUMNS 19549, collected 10 July 1968 by R. Thomas. 0.5km E Bellavista, 1km W Río Marañon, 1725ft [526m]: LACM 49419-20, 49423 (adult males), 49421-22, 49424-28, collected 24 November 1968 by J. W. Wright and J. R. Dixon. Perico: AMNH 28636-40, 28645-46 (adult males), 28641-44; MCZ 18789, 59277-79, 59282-85, 59287-310; MCZ 59280-81, 59286 (adult females); UMMZ 59025a-d (adult male, two adult females, one subadult); MCZ 18784-86, 18788 (skeletons); all collected September 1916 by G. K. Noble and the Harvard Peruvian Expedition. Fundo Atapaca, Río Chinchipe, E of San Ignacio, 450m: KU 209513-15, collected 4 October 1986, collector unknown. Río Chunchuca, 29km S, 13km W Jaen: MVZ 82316-17, collected 29 August 1967 by R. B. Huey. 28km N Santa Cruz, 725m: LSUMNS 19544-48, collected 11 July 1968 by R. Thomas.

PERU: DEPTO. AMAZONAS: 8km WSW Bagua, 1500ft. [457m]: MVZ 82312, 82315 (adult females), 82369 (adult male), 82313-14, collected 22-23 August 1967 by R. B. Huey. San José (Bagua Grande): MCZ 165318, 165322 (adult females), 165321 (adult male), 165320, collected by P. Hocking 3 November 1982. 12km NE Milagro, 475m: LSUMNS 19550-51, collected 15 and 23 July 1968, respectively, by R. Thomas and K. P. Able. 1km NE La Peca, 2800ft. [854m]: LSUMNS 37010 (adult male), collected 7 August 1978 by M. D. Williams. La Peca, 920m: KU 212630 (adult male), collected 28 January 1989 by W. E. Duellman.

DISTRIBUTION (Fig. 4).— *Stenocercus huancabambae* is known from localities along the upper Río Marañon and its major tributaries (Río Chinchipe, Río Chamaya, Río Huayllabamba, Río Utcubamba) in northern Amazonas and Cajamarca departments, Perú. All known localities are below 1000m (actual range about 200m-920m) in the subhumid "Huancabamba Deflection" area of northern Perú.

The distribution of *Stenocercus huancabambae* possibly extends further west into the valleys of the Río Huancabamba and Río Chotano. There its range may abut or overlap that of *Stenocercus percultus* (known from near the Abra de Porculla; see species account for *percultus*). However, the numerous specimens of *Stenocercus huancabambae* from localities below 1000m in the Huancabamba Deflection region, and corresponding lack of specimens of *S. percultus* from the same sites, suggest that these two species do not occur sympatrically in this area. Distributional evidence suggests that *S. huancabambae* occupies more arid habitats than *S. percultus*, but the lower elevational range of *S. percultus* in more arid habitats has not been explored (see species account for *S. percultus*). *Stenocercus huancabambae* is apparently broadly sympatric with *Tropidurus stolzmanni* throughout its range (Dixon and Wright 1975).

ETYMOLOGY.—The name *huancabambae*, a noun in genitive case, is derived from the geological term "Huancabamba Deflection" used to describe the general area from which all specimens of *Stenocercus huancabambae* have been collected. It is named for the Río Huancabamba and the town of Huancabamba located in the Cordillera Occidental near the continental divide in this region. The main axis of the Andes changes orientation in this area (northwest to northeast trending, hence "deflection").

DATA ON THE HOLOTYPE.— Snout-Vent length, 87. Tail length, 194. Total length, 281. Midbody scales, 44. Gulars, 19. Internasals, 6. Subdigital lamellae on 4th finger and toe, 18 and 25, respectively. The lower jaw is slightly damaged at the union of the mandibles.

CHARACTERIZATION.— *Stenocercus huancabambae* is distinguished by the follow-

ing combination of features: (1) Dorsal head scales keeled; many multicarinate, especially the supraoculars; (2) distinct parietal, interparietal, and postparietal scales; posterior head scales large; (3) Internasals usually 6, occasionally 5; (4) One row of enlarged supraoculars; (5) a single canthal on either side between the superciliaries and the small postnasals or nasal; (6) two (occasionally three) projecting, blade-like, angulate temporal scales in line with the superciliary row, and separated from the posterior dorsal head scales by at least one row of small scales; (7) Gulars weakly keeled; ventrals weakly to moderately keeled; (8) Parietal eye distinct; (9) Neck folds weakly developed to absent; (10) Paradorsal scales large, imbricate, mucronate, and moderately keeled; (11) Prominent serrate vertebral crest in adult males; weakly developed in females; (12) Deep posthumeral and postfemoral pockets; Types 4 and 5, respectively (Fig. 3); (13) Scales on posterior surface of thigh imbricate, keeled; (14) Tail very strongly compressed, in larger adult males deeper somewhat posterior to the pelvis than at the pelvis; (15) Males and females have a light vertical bar in front of the forelimb insertion extending onto proximal forelimb; dark scapular spot in adult males, obscure to absent in females; dark pigment on throat and ventral surfaces of head, if present, usually limited to a dark midventral patch on throat (males), or occasionally dark streaking on throat; some males with a broad dark lateral stripe from the head to the hind limbs.

COMMENT.— Based on the possession of (1) large posterior head scales, (2) large supraoculars, and (3) keeled ventral scales, *Stenocercus huancabambae* matches the external criteria of the genus *Ophryoessoides*, as outlined by Fritts (1974). It is the only species here described which does so.

DIAGNOSIS.—*Stenocercus huancabambae* differs from all members of the genus *Stenocercus* sensu Fritts (1974) by having (1) enlarged, keeled posterior head scales with distinct parietal, interparietal, and postparietal scales; (2) one row of greatly enlarged supraoculars; (3) keeled ventrals; and (4) a greatly compressed tail. No species of *Ophryoessoides* sensu Fritts (1974) has the combination of (1) two projecting, blade-like, angulate temporal scales, (2) keeled or multicarinate dorsal head scales and supraoculars, (3) weakly or moderately keeled gular scales, (4) six internasals (usually), (5) a single canthal scale, (6) strongly keeled paradorsals, and (7) a very strongly compressed tail in adult males.

DESCRIPTION.—*Head* (Fig. 8). Dorsal head scales keeled or multicarinate, generally juxtaposed and only slightly protuberant in large adults. Rostral large, with projecting tip dorsomedially; in contact with the first supralabials, the first lorilabials, and (usually) four postrostrals. Medial postrostrals longer than wide, narrowly in contact with the rostral, and each usually in contact with three or four internasals. Generally six internasals (occasionally 5, infrequently 4 or 7). Nasals separated from first supralabial by the first lorilabial; generally separated from rostral by postrostrals (nasals rarely in contact with rostral, e.g., AMNH 28640, 28643, MCZ 59280). A single canthal in front of the superciliary series, separated from nasal by a series of very tiny scales. Three to four elongate superciliaries overlapping posteriorly, followed by two shorter posterior superciliaries overlapping in the reverse direction. Four to five (occasionally only three) transversely-broadened supraoculars, nearly always separated from the supraorbital semicircle by a row of very tiny scales (rarely in contact, e.g., LACM 49419). Width of broadened supraoculars usually not more than twice their length. The largest supraocular at least twice as large (usually more) as any supraocular in other rows. Supraorbital semicircles in broad contact. Supraoculars multicarinate. Distinct parietals, interparietal, and postparietals; the parietals in contact behind the interparietal. Parietal eye distinct in all individuals. A row of two or three occipital scales present between parietals and dorsal neck scales. On each side, two strongly keeled, blade-like, angulate temporal scales posterior to the dorsal border of the eye, and in line with the superciliary row (ap-

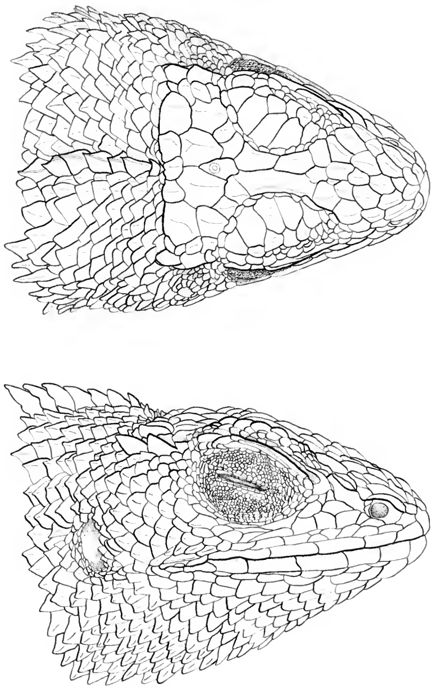

Fig. 8. *Stenocercus huancabambae* (Holotype, male, SVL 87, MCZ 165319). Dorsal and lateral views of head. Perú: Depto. Amazonas: San José (Bagua Grande). Drawn by G. Bisbee.

pearing as sharply keeled, but without projecting blade, in juveniles); occasionally a third small scale is also so-modified. (In adults, these scales differ from the elongate keeled scales in a similar position in adults of *S. percultus* in that the projecting portion is thin and blade-like in *huancabambae*, whereas in *percultus* there is no free projecting blade). The angulate temporals are separated from the large posterior head scales by a single or partially doubled medial row of small keeled scales. Lateral temporals small, weakly keeled, and imbricate. Anterior and posterior gular scales weakly keeled. Mental in contact with two postmentals and the first pair of infralabials. The first pair of postmentals is followed by a series of two to three large postmentals on each side.

Neck and body. Dorsal and lateral neck and body scales large, imbricate, mucronate, and moderately keeled; the keels pointing obliquely

posterodorsally. Ventral scales weakly to moderately keeled; ventral scales of females and subadults are more strongly keeled than those of adult males. Prominent serrate vertebral crest in adult males from nape to the anterior half of the tail; dorsal crest of females only weakly developed. Tympanum moderately recessed. Preauricular fringe weakly- to moderately-developed.

Neck folds. Neck folds very weakly developed to absent. A few individuals have traces of antehumeral, gular, and/or antegular folds, but these are not well-defined. A weak dorsolateral fold is suggested in some individuals, sometimes extending from the posterodorsal margin of the ear to the hind limbs. Other neck folds absent.

Tail. Tail very strongly compressed; in large (>80mm SVL) adult males it is deeper slightly posterior to the pelvic region than at the pelvic region. Scales unicarinate. Vertebral crest prominent on anterior half, thence decreasing in size.

Limbs. Dorsal and ventral scales of the forelimb moderately keeled. Dorsal scales of hindlimbs moderately keeled; ventral scales of hindlimb only weakly keeled. Scales on posterior surface of thigh imbricate, keeled. Supradigitals unicarinate; subdigitals multicarinate. Scales of the soles and palms multicarinate.

Dermal Pockets (Fig. 3). Posthumeral and postfemoral pockets Types 4 and 5, respectively. The posthumeral pocket is a deep depression with a broad opening, without a distinctly raised and thickened border of skin; it is lined with small pointed scales. The border of the opening of the posthumeral pocket is ringed by an array of long, sharply pointed scales. The opening of the postfemoral pocket is a slit less than half the height of the thigh. The pocket depth is equivalent to about five scales on its outer wall. It is lined by granular, pavement-like scales.

Pattern (Fig. 9; descriptions based on preserved specimens only). Dorsal head scales usually medium brown without darker markings, although occasional individuals have a thin dark brown interocular line. Males and females have a light antehumeral vertical bar about one scale wide that extends, in most individuals, onto the proximal part of the forelimb; anteriorly it is bordered by a thin dark line. Most individuals have some indication of a large dark scapular spot (generally prominent in males, obscure to absent in females; see comments on geographic variation below). A light dorsolateral stripe is present extending from the dorsal margin of the ear to the anterior third of the trunk, occasionally to the tail base. Some males have a broad dark irregular stripe extending along the flank from the corner of the mouth to the hind limbs. A dark elongate spot is present on the throat of some adult males (see Sexual Dimorphism and Geographic Variation).

Scale counts and measurements (Tables 1 and 3). The body scales, including those of the dorsal crest, are very large, resulting in low meristic values. The tail is much more than twice the body length.

Size and sexual maturity. The largest male (MCZ 18791) has a SVL of 95; the largest female (MCZ 165322) has a SVL of 75. The smallest male showing the distinctive coloration of the adult (MVZ 82369) has a SVL of 70.

Sexual Dimorphism and Geographic Variation. Males attain a larger size than females, have a higher vertebral crest, and a considerably more compressed tail. In females the tail is rounded and does not bear a crest composed of enlarged vertebral scales, whereas in males the extreme compression of the tail is exaggerated by the presence of enlarged vertebral scales for about half its length. All population samples are quite similar in meristic data (Table 3).

Adult males have a large, well-defined dark brown scapular spot (see Coloration and Fig. 9) that is smaller and less distinct (not apparent in some preserved specimens) in females. The spot appears in many subadults (e.g., MCZ 59278, 59285, 59290, 60036; SVLs 49-51); all individuals in this size range bearing a distinct scapular spot for which the sex was checked by dissection were males.

Adult males (AMNH 28636-40, 28645-46; UMMZ 59031, 59025) and some subadults,

Fig. 9. *Stenocercus huancabambae.* Male (above) and female (below) from Perú: Depto. Amazonas, San José (Bagua Grande). Photographs by P. Hocking, courtesy of E. E. Williams.

presumably males (MCZ 59278-79, 59284-85, 59290; UMMZ 59031, 59025) from Perico and Bellavista, Depto. Cajamarca, usually have a dark brown (in preservative) longitudinally elongate irregular spot on the throat. A faint version of this spot is present in some males from other populations (e.g., MCZ 60036, 165321; LSUMZ 19544), but not in several large adult males from various localities: MCZ 165319 and LSUMZ 37010, both from the Río Utcubamba drainage, and MCZ 18791-93 and LACM 49419 from (or near) Bellavista, Depto. Cajamarca. No adult females had the throat spot.

COLORATION.— *Coloration in life.* Few notes are available on coloration in life for *Stenocercus huancabambae.* The tag of LSUMNS 37010 (adult male, SVL 82) states: "scales on belly and throat pink." The scales on the throat and belly of the following adult males are pinkish in preservative, but might have been brighter in life: LACM 49419, AMNH 28638, KU 212630, MCZ 165321 (belly only), and the holotype. The ventral scales on the proximal half of the tail of the holotype bear a pinkish wash. The dorsal coloration of MVZ 82312 (adult female, SVL 60) was described as "chestnut" (R. B. Huey, field notes in MVZ).

Coloration in Preservative (see Fig. 9). Adult males.— Dorsum medium brown or grayish brown with a dark brown bar or chevron middorsally above the forelimbs; other dark chevrons are sometimes present on the body (e.g., KU 212630). Occasionally, other dark brown flecks are present dorsally, particularly on the neck. The top of the head is brown or grayish brown with a dark brown bar extending between the anterior portions of the eyes. A dark brown bar extends diagonally upward across the temporal region from the posterodorsal edge of the eye to cover the lateral edges of the angulate temporal scales. Some individuals have other irregular light and dark brown flecks on the dorsal surface of the head. Laterally, a dark brown spot or ocellus (6-10 scales in horizontal diameter; slightly greater in vertical dimension) is present in the scapular region. This spot is bordered anteriorly by a thin vertical grayish white bar that extends onto the proximal forelimb; this bar is bordered anteriorly by a thin vertical dark brown bar. A thin light stripe bordered below by a thin dark brown stripe extends from the posterodorsal border of the ear dorsolaterally along the body, merging with the dorsal ground color about 1/3 of the way along the trunk. Scales of the dorsal crest are grayish brown and dark brown. Dorsal scales of the tail in most individuals somewhat lighter brown than that of the dorsum; tail occasionally bears vague indications of darker spots or bars. The dorsal surfaces of the limbs are brown, generally without darker markings or vaguely barred with dark brown.

The entire ventral surface of adult males has a brown, yellowish-brown or grayish-brown wash. Some individuals retain evidence of col-

Table 3. Geographic variation for meristic characters among samples of *Stenocercus huancabambae*. Many specimens are hatchlings and subadults, so characters are not broken down by sex. Range (sample size), and mean±S.D. are given for each sample.

	Depto. Cajamarca			Depto. Amazonas
	Perico	Bellavista + Santa Cruz	Río Chunchuca	(all localities)
Midbody scales	37-48 (50) 42.4 ± 2.67	39-53 (45) 45.18 ± 3.12	45-47 (2) 46.0 ± 1.41	40-50 (13) 45.0 ± 2.77
Vertebral scales	37-50 (50) 42.64 ± 3.06	37-51 (45) 44.27 ± 3.53	43-47 (2) 45.0 ± 2.83	39-51 (13) 44.46 ± 3.71
Paravertebral Scales	48-64 (50) 54.68 ± 3.30	48-64 (45) 57.31 ± 3.52	61-62 (2) 61.5 ± 0.71	51-61 (13) 58.31 ± 2.69
Gular scales	18-24 (50) 20.6 ± 1.48	18-28 (43) 20.79 ± 1.85	21-23 (2) 22.0 ± 1.41	19-24 (13) 21.77 ± 1.48
Lamellae 4th finger	14-19 (50) 16.74 ± 1.34	14-20 (45) 16.98 ± 1.39	17-19 (2) 18.0 ± 1.41	14-19 (13) 16.08 ± 1.44
Lamellae 4th toe	21-27 (50) 24.18 ± 1.44	22-48 (45) 25.18 ± 1.39	27-28 (2) 27.5 ± 0.71	22-26 (13) 24.08 ± 1.26

oration on the belly in the form of a pinkish wash of varying intensity. This wash is sometimes divided midventrally with a dusky streak. Adult males often have a dark brown irregular spot, usually longer than wide, midventrally in the throat region (see above, Geographic Variation). Its width varies from about 2-1/2 scales to 8 scales.

One adult male (LSUMNS 37010) is much more boldly patterned than all other specimens. Some features of the pattern in this specimen (dark interocular and temporal bars, ocellae in the shoulder region bordered anteriorly by a light bar) are consistent features in other individuals of this species. LSUMNS 37010 has a more vivid pattern on the lateral surfaces of the head and body than other specimens. The gular and throat regions are dusky with darker streaks present laterally (similar throat patterns are present in many juveniles of the type series and in another adult male, KU 212630). A dark brown bar extends from the angle of the jaw to the proximal anterior surface of the forelimb. A dark brown facial stripe occupies portions of the upper and lower labials, extends posteriorly across the ear, and broadens to occupy 5-6 lateral scale rows. This stripe is interrupted in the shoulder region on each side by the ocellae, but then continues to the base of the tail as a broad lateral stripe with irregular upper and lower edges. Dorsolaterally, it is bordered by a light stripe extending from the temporal region to the base of the tail. The dorsum of LSUMNS 37010 is darker brown than other individuals, and bears indications of middorsal bars or chevrons from the neck to the base of the tail. Dorsally, its tail is yellowish brown with irregular dark brown flecks and streaking, concentrated laterally and ventrolaterally. The venter is grayish white to yellowish white with a grayish or brownish wash. A few other adult males (MVZ 82369; MCZ 165321; LACM 49419; the largest male of UMMZ 59031) and some subadults (UMMZ 59025 and 59031 se-

ries) from other localities have faint indications of the lateral dark brown stripe and/or throat streaking observed in LSUMNS 37010.

Females and subadults. The pattern is much more subdued than in adult males, and the ocellus and associated bars in the scapular region generally are less distinct (absent in some preserved specimens). The dark interocular and temporal bars, and the dorsolateral light stripes are present. Females and subadults usually have more dorsal chevrons than adult males. Two adult females (MCZ 165318, 165322; Depto. Amazonas: San José (Bagua Grande)) are greenish brown dorsally. These two females and a small (? adult) male from this locality (MCZ 165321) have dusky throats with indistinct dark streaking. Other females and subadults are brownish to tan dorsally, but the extent to which these color differences reflect preservational differences is not known.

COMPARISONS.—*Stenocercus huancabambae* is similar in many respects to *S. percultus* but can be distinguished by characteristics of the scutellation and color pattern, which are detailed in the species account for *S. percultus*. *Stenocercus huancabambae* has been confused, at least occasionally, with *S. iridescens* (Gunther), a species of the coastal areas of western Ecuador and northwestern Perú (Fig. 4). Noble's series in the AMNH and MCZ were originally identified as *Leiocephalus* (now *Stenocercus*) *iridescens* (see also Burt and Burt 1931:269-270, who noted "much variation" in head scalation and vertebral crest development in their series of "*iridescens*," including Noble's specimens, but attributed no significance to the variation). These two species are quite distinct in numerous features, however. Gunther's (1859) description of *Stenocercus iridescens* is thorough, and includes a color plate of an adult male (Gunther 1859, Plate 20, Fig. B; see also Fig. 10). Only the major differences between *S. huancabambae* and *S. iridescens* (characteristics in parentheses) are noted here: Internasals 6, rarely as few as 4, usually some in contact with rostral (2, occasionally a tiny third one, not in contact with rostral); Two projecting, blade-like, angulate temporals (0); Many dorsal head scales and all supraoculars keeled (most dorsal head scales, and all supraoculars smooth); Posthumeral pocket deep, type 4 (shallow, type 1); Postfemoral pocket deep, type 5 (absent, type 1); Tail very strongly compressed (moderately compressed); No horizontal black bar across throat (present).

Stenocercus (*Ophryoessoides* sensu Fritts 1974) *aculeatus* and *scapularis* occur on the Amazonian slopes of Ecuador and/or northern Perú, and are superficially similar to *S. huancabambae*. *Stenocercus aculeatus*, in particular, resembles *huancabambae* in having two projecting, blade-like, angulate temporal scales and a single canthal scale between the anterior border of the eye and the nasal scale (see O'Shaughnessy 1879, 1881). Adults of *aculeatus* have the following characters that distinguish them from *huancabambae* (features in parentheses): smooth or, in juveniles, slightly wrinkled, head scales (keeled or multicarinate); smooth supraoculars (multicarinate); width of the broadened supraoculars usually much greater than twice their length (usually twice or less than their length); a distinct dorsolateral crest (in addition to the vertebral one) formed by a row of projecting scales and extending from the neck to the base of the tail (dorsolateral crest, when present, weak and restricted at most to neck and shoulder region); paradorsal scales only weakly keeled, or tending to be smooth anteriorly and keeled posteriorly (strongly keeled); throat of adult males black (at most, a black midventral spot). Juveniles of *aculeatus* and *huancabambae* are more difficult to distinguish because juveniles (and particularly hatchlings) of *aculeatus* have more strongly keeled scales on the head and body than do adults, thus making it more difficult to use this distinction between adults of the two species in the nature of the head scales and paradorsal scales. However, the dorsolateral crest in *aculeatus* is usually evident in juveniles, and the relative width of the supraoculars provides an additional distinguishing feature.

Stenocercus scapularis (see Boulenger 1901)

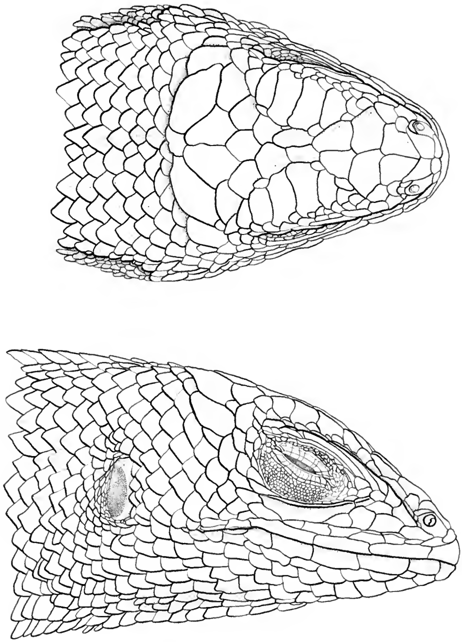

Fig. 10. *Stenocercus iridescens* (male, SVL 81, MCZ 154583). Dorsal and lateral views of head. Ecuador: Prov. Pichincha: Centro Cientifico Río Palenque, 47 km S Santo Domingo de los Colorados on road to Quevedo. Drawn by G. Bisbee.

has the following features that distinguish it from *huancabambae* (characteristics in parentheses): strongly keeled gulars and ventrals (weakly to moderately keeled); paradorsals smooth (strongly keeled); superciliaries that project over the eye (non-projecting); tail slightly compressed (extremely compressed in adult males); a well-developed dorsolateral crest on the body, at least anteriorly and in the sacral region (weakly developed; present, at most, in neck and shoulder region).

Stenocercus huancabambae can be distinguished from all other species of *Stenocercus* by the combination of (1) an extremely compressed tail that is slightly deeper posterior to the pelvic region than at the pelvic region in large adult males; (2) two projecting blade-like angulate temporal scales; and (3) 6 internasals. *S. huancabambae* is distinguished from most species of *Stenocercus* (sensu Fritts, 1974) occurring in northern Perú and southern Ecuador (*carrioni*, *chrysopygus*, *crassicaudatus*,

empetrus, *festae*, *haenschi*, *humeralis*, *ivitus*, *melanopygus*, *moestus*, *nigromaculatus*, *nubicola*, *orientalis*, *ornatissimus*, *simonsi*, *varius*) by the presence of a deep (type 4) posthumeral pocket (all of the above have, at most, a shallow posthumeral pocket, types 1-3) and enlarged posterior head scales. The three characteristics listed above, plus aspects of color pattern, will distinguish *huancabambae* from the two species of *Stenocercus* in southern Ecuador that have deep posthumeral pockets and projecting vertebral crests (*S. rhodomelas* and *S. ornatus*; see Comparisons under *S. percultus* for characteristics of these species).

OSTEOLOGY.— Dry skeletons of four specimens were available (sex and measurements prior to skeletonization not available; skull lengths are given): MCZ 18784 (20mm), 18785 (24mm), 18786 (22mm), 18788 (14mm). The eight osteological features discussed by Etheridge (1966) conform to the South American pattern. The dorsal roofing bones of the skull are smooth in the smallest specimen, but in the larger ones there is sculpturing on the parietal, frontals, prefrontals, and the upper part of the postorbital. The sculpturing has a clear correspondence to the overlying scale pattern (see Etheridge and de Queiroz 1988:291). The nasal-frontal contact is well-ossified, even in the smallest individual. The parietal foramen is persistent. The superior fossa of the quadrate is not enlarged. The tricuspid maxillary teeth are slightly compressed, unflared, and with blunt cusps. Pterygoid teeth are present, 3 per pterygoid in the smallest specimen, 6-9 in the larger ones.

NATURAL HISTORY OBSERVATIONS.— The vegetation of the general area from which *Stenocercus huancabambae* is known was described as "thorn scrub with mesquite (*Prosopis*), palo verde (*Cercidium*), and columnar cacti (*Cereus* and *Cephalocereus*) dominating" (Dixon and Wright 1975:36); this corresponds to the "macrothermal rainy-green region" of Weberbauer (1936:67). However, *Stenocercus huancabambae* may be limited to more specific microhabitats within this area. The tag of LSUMNS 37010 states "shot in hedgerow on hillside near rice fields," hence in disturbed habitats.

The following notes describe specific habitats where *S. huancabambae* has been collected (R. B. Huey *in litt.*, quoted from field notes for 21-23 August 1967, 8km WSW Bagua, Depto. Amazonas, Perú): ". . . camp along a small stream and bridge. . . habitat here was mixed forest (deciduous) interspersed with lots of cacti — prickly pear and "*Cereus*" types. Some areas with trees over 40ft. tall. In tearing apart one rotten log I found an almost chestnut colored iguanid [MVZ 82312] under bark of rotting log 6" diameter. The day was chilly and no others seen. (Aug. 23): . . . others [iguanids] seen in areas of leaf litter and moderate shade . . . , two as above [in logs], with another male in . . . fallen cacti logs. *Ameiva* were thick in the more open areas." Additional notes describe the habitat for MVZ 82316-17 as follows (R. B. Huey *in litt.*, quoted from field notes for 29 Aug. 1967, Río Chunchuca, 29km S, 13km W Jaen, Depto. Cajamarca, Perú): ". . . a riparian deciduous forest with the canopy about 25 meters . . . lots of leaf litter 2-3" thick under the trees . . . flushed two iguanids from under logs in the leaf litter."

The descriptions of specific habitats for *Stenocercus huancabambae* suggest a somewhat more arid environments for this species than known habitats for *S. percultus*. Thus, if the ranges of these two species abut near the Abra de Porculla (see above), the two species may be segregated by habitat.

One female from the Abra de Porculla (MVZ 82315; SVL 62 mm) collected 23 August 1967 contained two thin-shelled ova. Numerous individuals of the type series from Perico and Bellavista (Depto. Cajamarca; all of these in MCZ) and one individual from near Bagua (Depto. Amazonas; MVZ 82314) are close to hatching size (SVLs 29-35 mm). All of these were collected during the dry season ("summer and autumn 1916" for the Perico and Bellavista specimens [Barbour and Noble 1920b:395], and 22-23 August 1967 for MVZ 82314).

***Stenocercus imitator*, new species**
(Figs. 11-14)

HOLOTYPE.— FMNH 232634 (field number J. E. Cadle 7771), an adult male, collected 23 May 1987 from the road above Monte Seco toward Chorro Blanco, approximately 1.5km (airline) NE Monte Seco, 1450m, Río Zaña, Departamento Cajamarca, Perú. Chorro Blanco is a prominent waterfall near the site of Cadle's field camp (Fig. 6). The road between Monte Seco and Udima passes through the village of El Chorro (1km N Monte Seco) and heads roughly northeasterly in the direction of Chorro Blanco before turning abruptly westward to ascend the slope to Udima. The type locality is along the road E of the village of El Chorro before its abrupt turn toward the west (Fig. 6).

PARATYPES (unless otherwise noted, collected by J. E. Cadle).— PERU: DEPTO. CAJAMARCA: RIO ZAÑA: El Chorro-Udima Rd., approximately 3km (airline) N Monte Seco: 2200-2400m: FMNH 231780 (adult female), 231784 (adult male), 231786 (adult female); 2130m: 231781-83 (adult females), 231785 (adult male); (all collected 23 June 1987); 2210-2240m: 232611, 232616, both subadults; 2310m: 232650 (adult male); all collected 8 June 1987; 2000-2200m: 232625, 232635 (adult males); collected 31 May 1987; Monte Seco-Udima Rd., approximately 2.5km N (airline) Monte Seco: 2100-2300m: ANSP 31726, 31728, 31731, 31733-35 (all subadults), 31727, 31732, 31736 (adult females), 31729-30, 31737 (adult males), all collected 17 January 1989; Monte Seco-Udima Rd., approximately 2.5km N (airline) Monte Seco: 2450m: ANSP 31738 (adult female), 31739 (adult male; cleared and stained plus skin) collected 17 January 1989. 0.5km by rd. E to NE El Chorro (=1km NE [airline] Monte Seco): 1440-1490m: FMNH 232584-85 (adult males; skins and associated dry skeletons), 232587 (adult male; skin and associated dry skeleton), 232590 (adult female; skin and associated dry skeleton), 232609-610, 232612 (all subadults), collected 17 June 1987; 1450-1460m: ANSP 31720, 31722 (adult males), 31721 (subadult), collected 16 January 1989; 31724-25 (adult males), collected 20 January 1989. Approximately 1.5km (airline) NE Monte Seco on El Chorro-Udima Rd., 1450-1480m: FMNH 232648 (adult male), collected 23 May 1987; FMNH 232657 (adult female), collected 13 June 1987. Rd. just E El Chorro, approximately 1-2km NE (airline) Monte Seco: 1450m: FMNH 232613 (subadult), collected 13 June 1987; 1500m: ANSP 31743, 31746 (subadults), 31744 (adult female), 31745 (adult male), collected 18 January 1989. Trail between Monte Seco and Chorro Blanco, approximately 2km (airline) NE Monte Seco, 1550-1570m: FMNH 232623, 232628, 232647, 232658-59 (all adult males), 232649 (adult female), collected 12 May 1989. Trail between Monte Seco and Chorro Blanco, approximately 1-2km NE (airline) Monte Seco: 1400-1500m: FMNH 232632, 232652, 232661 (all adult females), collected 30 May 1987; 1500m: ANSP 31740-42 (all subadults), collected 15 January 1989; 1550m: ANSP 31719 (adult female), collected 13 January 1989; 1600m: ANSP 31747-49, 31752 (subadults), 31750-51 (adult males) collected 18 January 1989. Approximately 1km (airline) S to SSW Udima, Río de Udima, 2500m: FMNH 232615 (subadult) and 232645 (adult female), collected 20 May 1987; FMNH 232629, 232631, 232636, 232638, 232655 (all adult males), collected 8 June 1987. Trail between Monte Seco and Chorro Blanco, approximately 2.5km (airline) NE Monte Seco, 1750-1800m: FMNH 232586 and 232588 (adult males; skins and associated dry skeletons), 232619 (subadult), 232620, 232651 (adult females), 232656 (adult male), 232660 (adult male; skin), 232662 (subadult), collected 11-27 May 1987; ANSP 31714 (subadult), 31715-18 (adult males), collected 13-14 January 1989. 2.5km (airline) NE Monte Seco, 1690m: FMNH 232642 (adult female), collected 26 May 1987; Vicinity of Monte Seco, 1300m: FMNH 232622, 232624, 232643 (adult males), 232641, 232654 (adult females), collected 17 May 1987; Vicinity of Monte Seco, 1200m: FMNH 232639 (adult male), collected 11 May 1987, ANSP 31723 (subadult), collected 20 January 1989; Trail between Quebrada Chorro Blanco S toward Monte Chico, approximately 2km (airline) ENE Monte Seco, 1570-1590m: FMNH 232614 (subadult), 232640, 232653 (adult males), collected 6-7 June 1987. Trail between Quebrada Chorro Blanco S toward Monte Chico, approximately 2km ENE Monte Seco, 1580-1640m: FMNH 232621 (adult male), 232627, 232633, 232644, 232646 (adult females), collected 14 May 1987. 35 mi. WNW Cajamarca, 6000ft. [1830m]: MVZ 89894-95 (subadults), 89896-97 (adult females), collected 23-25 August 1969 by R. Hilborn, C. B. Koford, and M. Leong (field notes of C. B. Koford in MVZ indicate that this locality is in the Río Zaña valley along the road between La Florida and Taulis, a hacienda of the upper Río Zaña east of Monte Seco).

PERU: DEPTO. PIURA: 2km W Porculla Pass (30km ENE Olmos), 6500ft.[1980m]: MVZ 82370 (adult male) collected 31 August 1967 by R. B. Huey; MVZ 89893 (subadult male) collected 17 August 1969 by M. Leong. 2.8km by rd. SW Abra Porculla, 6500ft.[1980m]: LSUMNS 35232-35233 (adult females) collected 2 October 1977 by T. S. Schulenberg. About 15km by rd. E Canchaque on Huancabamba Rd., about 5700ft.[1737m]: MCZ 174163 (adult male) collected 9-10 December 1974 by R. Thomas; LSUMNS 27212, 27219-20 (all adult males); LSUMNS 27213-15, 27217, 27222, SDSU 1534 (all adult females), all collected 4 December 1974 by R. Thomas. 15km E Canchaque, 1850m: KU 181912-13 (adult males), 181914-16 (adult females) collected 26 February 1979 by W. E. Duellman.

DISTRIBUTION (Fig. 4).— *Stenocercus imitator* is known from three general localities on the Pacific versant of the Cordillera Oriental in northern Perú between 5° and 7° S latitude (near Canchaque and the Abra de Porculla, both in Depto. Piura; and upper Río Zaña, Depto. Cajamarca). The documented elevational range is 1200m to about 2600m, which is the known elevational range in the local area of Monte Seco (Río Zaña, Depto. Cajamarca).

ETYMOLOGY.— The specific epithet, *imitator* (= "mimic" or "imitator"), a Latin noun in apposition refers to the resemblance between this species and *S. praeornatus*, known from Depto. Junín in central Peru (Amazonian versant).

DATA ON THE HOLOTYPE.— Snout-vent length, 95. Tail Length, 224. Total length, 319. Scale rows around midbody, 100. Scales across the gular region, 37. Internasals, 4. Supraoculars, 4. Subdigital lamellae on the 4th finger and toe, 23 and 35, respectively.

CHARACTERIZATION.— (1) dorsal head scales smooth to slightly rugose, but not distinctly keeled except posterolaterally; (2) no distinct parietals, interparietal, or postparietals; posterior head scales small; (3) internasals usually 4, occasionally 3 or 5; (4) one row of supraoculars slightly broadened transversely (occasionally a second row is also somewhat broadened); (5) two canthals on either side between the superciliaries and the small postnasals or nasal; (6) no projecting, blade-like, angulate temporals; (7) gular scales smooth; (8) parietal eye not visible; (9) lateral skin of neck strongly folded; a weak gular fold present; (10) middorsal scales imbricate, strongly keeled, and grading abruptly into granular lateral scales; (11) vertebral scales form a serrate, moderately-projecting dorsal crest in adult males, weak in females; (12) posthumeral pocket inconspicuous or absent (type 1-2); postfemoral pocket deep, with a slit-like opening (type 5); (13) scales on posterior surface of thigh granular; (14) tail moderately compressed, without prominent spines; (15) strong sexual dimorphism in color and pattern; males with bold black series of blotches or irregular bars on neck and anterior trunk, and a broad black transverse band ventrally across the anterior pectoral region; belly of males lavender or rose-colored; females brownish with middorsal dark brown blotches or chevrons.

DIAGNOSIS.— *Stenocercus imitator* differs from all species of *Ophryoessoides* sensu Fritts (1974) in lacking enlarged posterior head scales and keeled ventral scales, and in having a relatively more rounded tail. It can be distinguished from all other species of *Stenocercus* by having the combination of (1) absent or weakly-developed posthumeral pockets (Type 1-2), and well-developed postfemoral pockets (Type 5); (2) well-developed series of neck folds; (3) granular scales on the posterior surface of the thigh; (4) a broad black band across the anterior pectoral region in adult males; and (5) a projecting serrate vertebral crest in adult males which extends from the nape onto the base of the tail.

DESCRIPTION.— *Head* (Figs. 11-12). Dorsal head scales small, juxtaposed, generally lying flat in females and subadults, slightly protuberant in adult males; smooth to slightly rugose (adult males), but not keeled except posterolaterally in the parietal region. Dorsal scales in antorbital region larger than those posterior to the orbits. Rostral rounded or pointed dorsally, in contact with the first supralabials, first lorilabials, and two or three

postrostrals. Postrostrals are much wider than long, unless there are three, in which case two are much larger than the third. Nasals separated from rostral and first supralabials by the first lorilabial. Internasals nearly always 4 (N=115); about 11% of the specimens has 3 internasals; percentagewise, most of these (4/18 specimens), are from the Canchaque and Porculla (northern) populations; another 2.6% of all specimens has 5 internasals. Two canthals in front of the superciliary series, the first in contact with the nasal or separated from it by tiny scales. Three or four elongate superciliaries overlapping posteriorly, followed by two shorter posterior superciliaries overlapping in the reverse direction. One row of supraoculars slightly to moderately broadened, separated from the supraorbital semicircle by a partial or complete row of small scales (sometimes partially doubled); if the enlarged supraocular row contacts the supraorbital semicircles, it is usually via one or two anterior scales of the row. Supraoculars smooth. Supraorbital semicircles in contact via two or three scales; the semicircles are highly irregular and not always distinct. No distinct parietal, interparietal, or postparietal scales. Posterior head scales small, irregular, and highly variable among individuals. Parietal eye not visible. Lateral temporal scales juxtaposed, rugose to keeled, merging gradually with the dorsolateral head scales. Scales of gular region and throat smooth. Mental in contact with the first pair of postmentals, the first infralabials, and occasionally one or two small median gulars or the first sublabial. The first pair of postmentals are in contact medially (rarely separated by small scales), and with the first infralabials and sublabials. Three to four large postmentals follow the first postmentals on each side.

Neck and body. Dorsolateral neck scales small, keeled, bluntly pointed, and slightly imbricate. Lateral neck scales granular, separated from the dorsal neck scales by 1-3 rows of small projecting pointed scales occupying the supra-auricular fold and dorsolateral fold (fold more prominent in males than in females). Paradorsal scales larger than dorsal neck scales, imbricate, strongly keeled, abruptly grading into small granular lateral scales. Lateral scales abruptly meet the ventral scales, which are smooth. Ventral scales equal to, or slightly smaller than, dorsal scales. Adult males with moderately developed projecting vertebral crest from the nape to the middle of the tail; crest in females and subadults less well-developed but still evident. Tympanum shallowly- to moderately recessed. Preauricular fringe absent or very reduced (females and subadults) to moderately-developed (adult males).

Neck folds. Skin of lateral neck region extensively folded in both sexes, but usually more developed in large males. Prominent dorsolateral, supra-auricular, and longitudinal neck folds; the dorsolateral folds may extend half the body length. Antehumeral fold continuous with a prominent gular fold that extends ventrally onto the pectoral region; gular folds of opposite sides usually widely separated midventrally, but may be closely approximated (e.g., FMNH 232624, 232639). Prominent ventrolateral (see Fig. 13) and (usually) posthumeral folds. Prominent oblique neck fold, continuing ventrolaterally as a longitudinal extension in front of the antegular fold. One to three supernumerary oblique neck folds. Antegular folds weakly developed, but may be prominent (e.g., FMNH 232639) or absent (many smaller individuals). Postauricular and rictal folds prominent.

Tail. Moderately compressed; covered dorsally and ventrally with keeled, mucronate scales except for a smooth postanal series. Vertebral crest prominent on anterior half.

Limbs. Dorsal scales of fore- and hindlimbs keeled. Ventral scales of forelimbs smooth to weakly keeled, and very small on upper forelimb. Ventral scales of hindlimbs smooth. Scales on posterior surface of thigh granular. Supradigitals of forelimbs smooth, of hindlimbs unicarinate. Palmar and plantar scales unicarinate. All subdigitals multicarinate.

Dermal Pockets. Posthumeral pocket Type 1 or 2. Postfemoral pocket Type 5. The posthumeral "pocket" consists of, at most, 3-4 small wrinkles in the skin, possibly artifactual, just behind the limb insertion (in some indi-

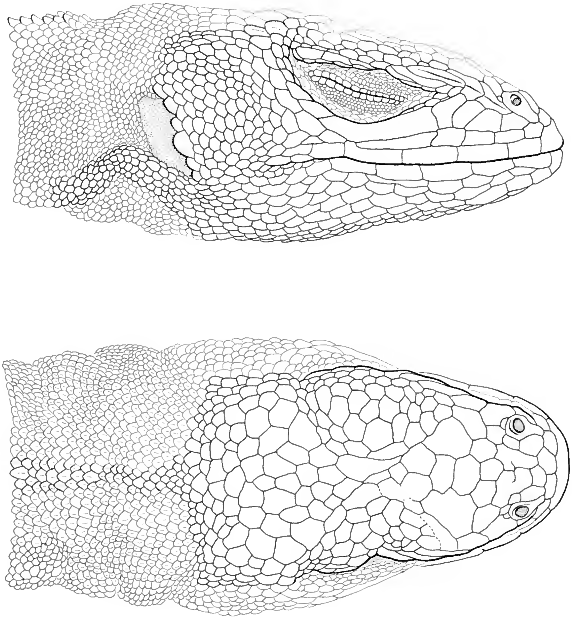

Fig. 11. *Stenocercus imitator* (male, SVL 89, MCZ 174163). Dorsal and lateral (left side, reversed) views of head. Perú: Depto. Piura: about 15km by road E Canchaque on Huancabamba Rd., about 5700 ft. (1737 m). Drawn by L. Meszoly, used with permission of E. E. Williams.

viduals, no wrinkles are apparent). No apparent modification of the skin surface was observed; this area was covered by granular scales similar to adjacent body scales. Mites (never in abundance) were observed attached at scattered locations among these wrinkles. Where there were mite concentrations, the skin was thickened and the scales appeared less keratinized.

The postfemoral pocket is deep and has an oblique, slit-like opening (broader in some individuals). The skin covering the posterior wall of the pocket is covered by granular scales somewhat larger than those on the posterior surface of the thigh. The lining of the pocket consists of granular pavement-like scales peripherally, and bare skin more deeply.

Pattern (Figs. 13-14). **Males**: head unicolor or with light lateral spots. Dorsum with bold black transverse series of blotches or irregular crossbands on neck and anterior trunk, each with light border, these fading posteriorly. Vertical rows of light spots on flanks. Ven-

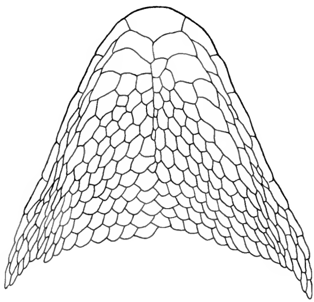

Fig. 12. *Stenocercus imitator* (male, SVL 89, MCZ 174163). Ventral view of head. Drawn by L. Meszoly, used with permission of E. E. Williams.

trally, a prominent black bar across pectoral region in front of forelimbs. Belly rose-colored to lavender in life, without dark markings. **Females**: Brown above with dark brown chevrons or cross bars. Lateral surface of neck and a triangular patch between the angle of the jaw and the ear often black. Gular region usually black or dark gray, occasionally grayish white. Belly whitish with varying amount of gray.

Scale counts and measurements (Tables 1 and 4). The lateral neck and body scales are very small, resulting in high meristic values. The tail is much more than twice the body length.

Size and sexual maturity. The largest male (FMNH 232638) has a SVL of 100mm; the largest female (ANSP 31744) has a SVL of 87mm. The smallest individuals showing evidence of the adult male coloration (see detailed descriptions below) have SVLs of 53-57 mm (ANSP 31717-18, 31723, 31730, 31749, 31752). These individuals show such male characteristics as accentuation of crossbars in the scapular region, light spots in vertical lines along the flanks, the beginnings of a dark ventral collar, and pinkish belly coloration. Two similar-sized individuals (ANSP 31728, 31741; SVL 54 and 56 mm, respectively) are inferred to be females on the basis of having dark gular and lateral neck pigmentation (ANSP 31728 only) characteristic of adult females. Assuming that attainment of sexual maturity corresponds to the development of these secondary sexual characteristics, these observations suggest that sexual maturity in both sexes may be reached at about 55 mm SVL.

Sexual Dimorphism and Geographic Variation. The sexes are strongly dimorphic in coloration (Figs. 13-14; see below), but not significantly in size or meristic features (Table 4). Males from the Río Zaña are more strongly patterned and have higher vertebral crests than those from Canchaque (sample size for the Porculla population is too small to evaluate). In males from Canchaque only the lateral and dorsal black markings above the forelimbs are prominent, whereas in males from the Río Zaña usually two additional series of black markings behind the forelimbs are also prominent (Fig. 13). Whether these pattern differences reflect preservation differences, or are perhaps partly attributable to the greater number of males of larger size in the Río Zaña sample, is unknown. There is a tendency for northern populations (Porculla and Canchaque) to have slightly higher counts for some meristic features (Table 4), but this trend is not consistent in either direction or magnitude.

COLORATION.— *Coloration in Life. Adult males* (based on FMNH 232656; SVL 84; see Fig. 13). Dorsum rich brown with a profusion of bright yellow spotting, heaviest on the neck and anterior trunk. Black neck bar in front of forelimb bordered posteriorly by a bright yellow line. Circular black marking over scapular region and an irregular black marking on flank behind forelimb. Black irregular bar complete along sides and across dorsum nearly half way between fore- and hindlimbs. Posterior to this are four obscure dark brown/olive bars across dorsum, each bordered by a line of yellow spots. Light sky-blue patches in anterior part of middorsal crest. Head brown with some yellow spots below eye and on upper labials. Lower

Fig. 13. *Stenocercus imitator* (male, SVL 96, FMNH 232648). Perú: Depto. Cajamarca: Río Zaña, approx. 1.5km NE (airline) Monte Seco, 1450m.

labials and gular region yellowish brown (more yellowish on labials). Throat patch and belly bright lavender. Black collar across pectoral region bordered behind by brown patch. Ventral surface of forelimbs brownish; of hind limbs orangeish. Dorsal surface of tail dull green with olive/brown bars. Ventral surface of tail pale orangeish (most of tail missing).

The coloration of males varies principally in the intensity of various pigments, and in the distinctness of certain pattern features (yellow dorsal spots, throat collar, dorsal bars, etc.). The black dorsal bars are highly irregular in shape, usually consisting of a wide paravertebral portion and a strong constriction in the paradorsal region, which may or may not completely separate the dorsal portion from the wider lateral portion. If there is complete separation, then the dorsal pattern appears to consist of a middorsal series of blotches and a separate lateral series of blotches. The lavender to pinkish ventral color varies considerably in intensity, even among large adults (colors are not as bright in small males). Head coloration varied from medium brown to dark brown to gray; occasionally the head was bright green (e.g., FMNH 232634 [holotype]). Color notes for an adult male from the Porculla population (MVZ 82370; field notes of R. B. Huey for 31 August 1967) are essentially the same as given above, but the dorsal spots were "off white" rather than being bright yellow.

Adult females and subadults (based on female FMNH 232620; SVL 78; see Fig. 14). Dorsum rich brown with obscure reddish brown bars middorsally that do not extend onto flank; these bordered irregularly with some black pigment. Flanks dark brown with some black speckling. Yellow line beginning below eye continuing obliquely upward over tympanum and along border between rich brown of middorsal region and dark brown of flank; this line

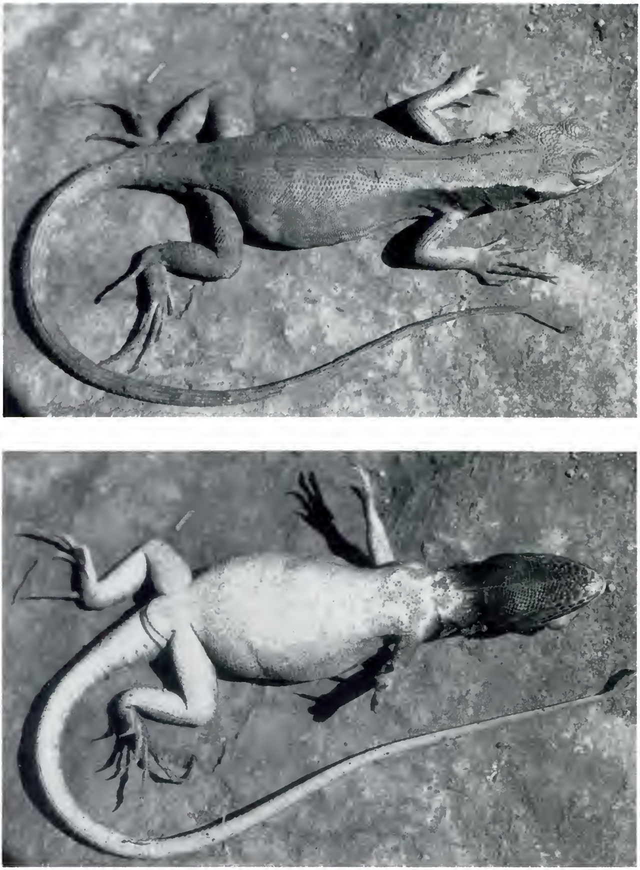

Fig. 14. *Stenocercus imitator* (female, SVL 80, FMNH 232645). Dorsal and ventral views of body. Perú: Depto. Cajamarca, 1km S (airline) Udima, Río de Udima (tributary of Río Zaña), 2500m.

Table 4. Geographic and Sexual variation for meristic characters and body size among populations of *Stenocercus imitator*. For meristic counts, range (sample size), and mean ± S.D. are given for each sex. Populations are indicated in Fig. 1.

		Depto. Cajamarca	Depto. Piura	
	Sex	Río Zaña	Porculla	Canchaque
Midbody scales	M	87-124 (43) 104.63 ± 8.05	104-110 (2) 107.00 ± 4.24	106-119 (6) 111.17 ± 4.71
	F	85-117 (27) 99.85 ± 9.31	105-113 (2) 109.00 ± 5.66	92-113 (8) 102.63 ± 7.44
Vertebral scales	M	49-64 (43) 56.12 ± 3.34	58-59 (2) 58.5 ± 0.71	58-71 (6) 63.5 ± 5.47
	F	50-64 (27) 57.04 ± 3.25	57 (2) 57.00 ± 0.0	58-73 (8) 64.63 ± 5.01
Paravertebral scales	M	89-112 (31) 101.09 ± 6.11	106-108 (2) 107.00 ± 1.41	102-116 (6) 108.83 ± 4.58
	F	92-119 (23) 102.87 ± 6.94	100-105 (2) 102.5 ± 3.54	98-114 (8) 106.63 ± 5.78
Gular scales	M	30-44 (42) 35.95 ± 3.36	36-43 (2) 39.5 ± 4.95	33-41 (6) 36.50 ± 3.08
	F	30-38 (27) 33.89 ± 2.31	31-33 (2) 32.00 ± 1.41	30-38 (8) 34.00 ± 2.62
Lamellae, 4th finger	M	21-25 (43) 23.26 ± 1.16	23-24 (2) 23.50 ± 0.71	22-25 (6) 23.5 ± 1.31
	F	19-26 (27) 22.85 ± 1.63	22-23 (2) 22.50 ± 0.71	20-23 (8) 21.50 ± 1.31
Lamellae, 4th toe	M	30-36 (43) 33.05 ± 1.54	32 (2) 32.00 ± 0.0	31-35 (6) 33.50 ± 1.52
	F	28-37 (27) 32.56 ± 2.04	31 (2) 31.00 ± 0.0	28-35 (8) 31.5 ± 2.45
Snout-Vent Length (mm)	M	53-100 (43)	38-84 (2)	56-89 (6)
	F	58-87 (27)	71-79 (2)	59-70 (8)

extends to about a third of the distance between fore- and hindlimb insertions. Entire dorsal surface of head medium brown. Upper surfaces of limbs and tail medium brown with black speckling, the speckling tending to form vague bars on thighs and shank. Lower labials and gular region pale yellow. Pectoral region white, grading into orangeish wash of belly, ventral surface of hind limbs, and tail. Ventral surface of forelimbs dull white with black speckling. Tail vaguely barred with two shades of brown. Lateral surface of neck brown with yellow line continuing from lower labials for about half way. A yellow spot half way between the end of the line and the forelimb insertion. A vertical yellow line just anterior to forelimb insertion extending from base of forelimb dorsally to meet dorsolateral yellow line.

There is much variation in coloration of females, particularly in the amount of pigment on the ventral surfaces and in the coloration of the head and dorsum. The following notes for FMNH 232645 (female, SVL 80) emphasize differences in coloration from the previously described female. The dorsum is grayish brown with reddish brown bars middorsally, continuing onto sides which are medium brown. Top of head medium brown. Light whitish line from top of tympanum to just past the forelimb insertion, and bordering the middorsal grayish brown area. Broad black band extending from corner of mouth, obliquely up to top of tympanum, and then bordering below the whitish dorsolateral line; lateral surface of neck entirely black. Lower labials, throat, and ventral surface of neck black with a pair of vague oblique white stripes extending from the throat under the corner of the mouth to the lower edge of the tympanum. Pectoral region and anterior belly mottled with dark gray and dirty white. Rest of belly grayish. Ventral surface of forelimbs grayish brown; of hind limbs whitish; and of tail white with a tinge of brown.

In general, the dorsal ground color of females ranges from greenish brown to light brown to grayish. Dorsolateral stripes are generally prominent from behind eye to at least above forelimb insertion, but their color varies from bright to pale yellow to grayish white to slate gray (e.g., FMNH 232652). The throat may be bright greenish yellow (e.g., FMNH 232632, 232661), slate gray with only the mental region greenish yellow (e.g., FMNH 232652), or grayish white. There is generally at least some indication of gray pigment just anterior to the sternal region. Venter is grayish white with gray speckling, greenish gray (e.g., FMNH 232661), or medium gray (but not as dark as throat; e.g., FMNH 232632, 232652).

Hatchlings (based on FMNH 232615; SVL 32). Dorsum brownish tan marked by transverse dark brown bands (vaguely forming parallel series of middorsal spots). Dorsum of head brown. Creamy whitish line from below eye, merging into tannish dorsal color. Sides of neck and body very dark brown (almost black). Dorsal surface of limbs dark brown; vague indication of barring on hind limbs. Upper labials creamy white with darker wash. Lower labials dark brown. Throat yellow with dark brown streaks. Venter dull whitish.

Coloration in Preservative. The dorsal ground color of males is grayish brown; of females brown, grayish brown, or gray. The dark dorsal blotches in both sexes persist, as does the ventral black collar of males. Light spots on the dorsum and throat of males fade to dull white. Head color of both sexes is brown to grayish brown. Ventral ground color of females grayish white, gray, or grayish brown, sometimes with lighter or darker reticulations. The throat of females is dark gray to black. Throat of males dark gray, usually with whitish spots and/or streaks (these are more evident in preserved specimens than in living individuals). The lavender pigmentation on the venter of adult males is persistent, being evident in specimens more than 20 years old (though greatly reduced in intensity). Many subadults (e.g., MVZ 89893-95) have dark gray throats with large white spots occupying multiple scales and/or a midventral white throat stripe.

Status of Stenocercus imitator VIS-A-VIS Stenocercus praeornatus.— Species Status. Fritts (1972, 1974) considered specimens of *S. imitator* from the vicinity of the Abra de Porculla

(a series of 5 in the Senckenberg Museum, which I did not examine, and MVZ 82370) conspecific with *S. praeornatus*, whose type locality is on the Amazonian versant of the Cordillera Oriental in central Perú (Comas: Depto. Junín). Since Fritts' work many more specimens of *imitator* have become available, including specimens from two additional populations. However, no populations geographically intermediate between the type localities of *praeornatus* and *imitator* are presently known. The elevation at the only known locality for *praeornatus* (3220m) is 600m higher than the highest known locality for *imitator* (2600m).

Although Fritts recognized some differences in scutellation and color pattern between the northern Peruvian specimens and the topotypic series of *praeornatus*, he did not consider the differences indicative of different species. My decision to recognize *imitator* as specifically distinct from *praeornatus* has not been easy or unequivocal because the two species are very similar in most morphological features traditionally used to distinguish species of *Stenocercus* (see Morphological Comparisons below). Nevertheless, consistent morphological differences do exist between topotypic specimens of *praeornatus* and samples of any of the known populations of *imitator*, and it is quite easy to assign specimens to one group or the other. Thus, despite some geographic variation in meristic features (documented above), populations of *imitator* are, overall, rather homogeneous in comparison to *praeornatus*. Moreover, the geographic distribution of *imitator* is one common to other amphibians and reptiles (unpublished data; cf. *Stenocercus percultus* and *S. chlorostictus* new species, described below), and plants (M. O. Dillon, pers. comm.) of northwestern Perú. Such shared geographic patterns suggest historical connectivity among populations of organisms in these forested communities of the Andean Pacific versant in northern Perú (see Discussion). It is partly to emphasize the historical connectivity suggested by the geographic distribution, and partly on the basis of consistent morphological differences between *imitator* and *praeornatus*, that I recognize *imitator*; see Frost and Hillis (1990) for a discussion of conceptual and practical issues concerning the delimitation of species boundaries.

Morphological Comparisons. Of those species of *Stenocercus* with an inconspicuous posthumeral pocket and moderately- to well-developed postfemoral pocket, *Stenocercus praeornatus* is the only species of *Stenocercus* with which *imitator* is likely to be confused (see Comparisons To Other Species, following). Fritts (1972; see also Table 1) noted that specimens of *praeornatus* (now *imitator*) from the Abra de Porculla had fewer scales across the gular region between the tympana than topotypic *praeornatus* (about 11 scales difference by my counts; Table 1), fewer scales around midbody (about 5 scales difference; Table 1), and that females from the Abra de Porculla lacked dark blotches on the chin (present in topotypic females of *praeornatus*). There are, however, other morphological differences between *praeornatus* and the known populations of *imitator*, although the arrangement of head scales in the two species is quite similar (compare Figs. 11 and 15).

In *Stenocercus imitator* the lateral scales are juxtaposed, granular, and unkeeled; under magnification they are squarish and have a distinctly knobby and raised appearance. In the type series of *S. praeornatus*, the lateral scales are imbricate or subimbricate, have angular posterior borders, and many retain evidence of keeling; under high magnification they lie flat. In males of *imitator* the vertebral crest is distinctly serrate, projecting from the nape onto the anterior 1/4 of the tail, and individual scales of the crest are at least as high, often higher, than long. In *praeornatus* the vertebral crest is serrate and distinctly projecting only on the neck and (slightly) at the base of the tail; otherwise the vertebral scale row forms a low middorsal keel. The individual scales of the crest in *praeornatus* are much less high than long. The comparison of crest size is most telling when comparing large males of *praeornatus* with relatively small males of

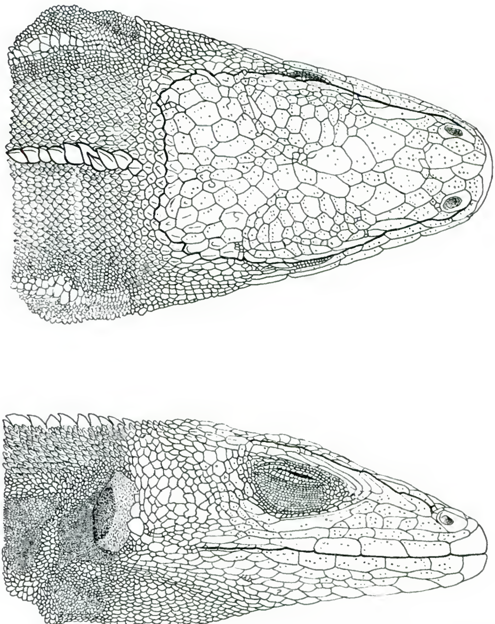

Fig. 15. *Stenocercus praeornatus* sensu stricto (male topotype, SVL 100, KU 134232). Dorsal and lateral views of head. Perú: Depto. Junín: Comas. Drawn by E. V. Malnate.

imitator: the former have a less projecting crest than the latter. Finally, the tail of *imitator* is somewhat more compressed than that of *praeornatus*, although this difference is subtle and not generally helpful except with series of both species available for comparison.

Females of *imitator* and *praeornatus* differ in one respect not evident in males. In *imitator* females the dorsal neck scales are very small, weakly keeled, weakly imbricate, and non-mucronate (sometimes almost appearing granular). In *praeornatus* females the corresponding scales are larger, mucronate, imbricate, and strongly keeled.

In addition to these qualitative differences in scale characters, *Stenocercus imitator* and *S. praeornatus* differ in many aspects of coloration, albeit many of the differences are ones of degree. Males of *S. imitator* are much more boldly patterned than those of *S. praeornatus* (compare Fig. 13 with Fritts' photo of *S. praeornatus* [1972:Fig. 2A; 1974:Fig. 30]). Males of *S. imitator* have minimally three bold black dorsal cross bands, the first above the

forelimbs, followed by two others; in most males a fainter (brown) series of crossbands continues posteriorly to above the hindlimbs. In some males of *imitator* from the Río Zaña these more posterior bands are also black, not as intense as in anterior bands, but still contrasting strongly with the dorsal ground color (gray to brown). Males of *S. praeornatus*, on the other hand, have at most a faint (brown) middorsal band above the forelimbs and faint brown blotches middorsally (Fritts 1972). The posterior part of the dorsum is dull gray or gray-brown. In males of *S. imitator* the vertebral crest has scattered light blue (whitish in preservative) scales forming a bold contrast with the black and brown scales of the crest. In preservative, scales of the crest in *S. praeornatus* males are uniform brown or gray for the most part. In *S. imitator* the light spots on the lateral surface of the head and neck are much smaller than those in *S. praeornatus*, in which the pattern is more regular and in which a light line tends to form along the supra-auricular fold by coalescence of a series of large light spots (easily seen in Fritts 1972:fig. 2A or 1974: fig. 30). In males of *S. imitator* the black ventral neck band is narrow, restricted to the area immediately anterior to the forelimbs, and more or less homogeneous in width across the ventral surface of the neck. In *S. praeornatus* males, this band is broader, extending anteriorly almost to the antegular fold and posteriorly to the level of the middle or posterior edge of the forelimb insertion; in addition, it is wider midventrally than laterally.

As is the case with males, females of *Stenocercus imitator* are more boldly patterned dorsally than are females of *S. praeornatus*. Many females of *S. imitator* have dorsal crossbands from the neck to the pelvis, whereas in *S. praeornatus* this pattern is obscure. The gular region of female *S. imitator* is gray-white to dark gray without barring (although some individuals with dark throat have light spots or streaks), and the chin is whitish. In *S. praeornatus*, there is usually dark gray barring, reticulations, or spots in the gular region, forming streaks somewhat parallel to the line of the jaw.

Distributional Comments. A distribution comprising populations on opposite sides of the Cordillera Occidental and Cordillera Oriental separated by 5° of latitude, as would be the case if *imitator* and *praeornatus* sensu Fritts (1972, 1974) were considered conspecific, would be highly unusual for a species of lizard. Fritts' (1972) comment that "... both localities from which the species [*S. praeornatus* sensu Fritts] is known are Amazonian ..." is erroneous — MVZ 82370, which he lists from "Abra Porculla" is actually from the Pacific versant to the west (see exact localities specified above; I have been unable to verify this for the Senckenberg Museum specimens). The presence of *S. imitator* on the Amazonian versant in the upper reaches of the Río Marañon or its tributaries is a possibility not yet documented by collections, although humid forest habitats suitable for this species possibly exist along the Río Huancabamba immediately east of the Abra de Porculla (see, e.g., Weberbauer 1945). Other than Fritts' suggestion that *S. praeornatus* (as he conceived it) and *S. boettgeri* shared similar distribution patterns, an erroneous inference (see below), I am aware of no other lizard species that have populations in northwestern Perú (Pacific versant) and central Perú (Amazonian versant). In fact, few other reptiles appear to have such a peculiar disjunct distribution. Snakes currently assigned to *Liophis epinephelus* are one possible herpetological example (see Dixon 1983; see comments on *Stenocercus boettgeri* below).

Since its description *Stenocercus praeornatus*, in the restricted sense used here, has been discovered at no localities other than the type locality. No specimens have appeared in the relatively well-known Río Tarma-Río Palca region (Depto. Junín) less than 80km to the north, from which specimens of at least four species of *Stenocercus* (*variabilis*, *boettgeri*, *crassicaudatus*, *formosus*) are available, though mainly at lower elevations than the type locality of *praeornatus*. This suggests that *praeornatus* has either a restricted range in the vicinity of the type locality (and perhaps further to the south, from where few *Stenocercus* specimens have

been collected), or a disjunct, but as yet unknown, distribution. Certainly, the distributions of *Stenocercus* species in the very complex mountainous terrain of Perú is not well-documented. The vast mountains separating the nearest localities for *praeornatus* and *imitator* (700km airline distance and very high chains of the Cordillera Oriental and Cordillera Occidental) could harbor other populations of either species which might provide additional evidence bearing on species status of these taxa. If such populations are eventually discovered, then re-evaluation of the status of *praeornatus* and *imitator* will be warranted.

Comments on Boulenger's Type Locality "Huancabamba." Fritts (1974) pointed out an apparent similarity in the distributions of *Stenocercus praeornatus* (as he conceived it) and *S. boettgeri* Boulenger (Type locality: "Huancabamba, Perú"); that is, both species apparently had peculiar disjunct distributions with populations in the northern Andes of Perú and in central Perú. Fritts apparently assumed that the type locality of *S. boettgeri* was the town of Huancabamba in the department of Piura, although this was not specified in the original description. Other species described by Boulenger (1911) from this type locality in the Boettger Collection have sometimes been assumed to be from the town of that name in Piura Department. However, Barbour and Noble (1920a), in discussing the distribution of *Prionodactylus spinalis* Boulenger (which was described in the same paper as *Stenocercus boettgeri*) commented: "Doctor Boulenger has informed us by letter that this [the type locality given as Huancabamba] was probably an error and that the specimens may have come from Oxapampa. If they came from Huancabamba, it was certainly from the Huancabamba of central but not that of northern Peru." The central Peruvian town of Huancabamba referred to is in the deparment of Pasco, about 25km northwest of the town of Oxapampa. Uzzell (1973) also concluded that the type locality of *P. spinalis* was Huancabamba, Department of Pasco, rather than the northern Peruvian town of the same name in the Department of Piura. *Stenocercus boettgeri* and other species described from the Boettger Collection with the type locality "Huancabamba" have been collected from other localities in central (Amazonian), but not northern, Perú; some, e.g. *Lachesis chloromelas* (=*Bothrops oligolepis*), are also known from further south in Amazonian Perú. Thus, *Stenocercus boettgeri* is presently known only from central Perú in the departments of Pasco, Junín, and Huánuco, and its type locality should be "Huancabamba, Deparment of Pasco, Perú" (contra Fritts, 1974). This inference also applies to the type locality of other species described by Boulenger from the Boettger Collection from this locality (see list in Barbour and Noble 1920b:395).

Given the existence of the town of Huancabamba near Oxapampa, there seems little reason to follow Boulenger's suggestion that the types of *Prionodactylus spinalis*, *Stenocercus boettgeri*, and other amphibians and reptiles from the Boettger Collection with the type locality "Huancabamba" actually came from Oxapampa. In fact, it was Barbour and Noble (1920b:395) who suggested that Boettger's material be labeled "Oxapampa" rather than "Huancabamba" in order to avoid the confusion created by having two towns of the latter name. This is a common problem with collecting localities in South America, but is not a justification for altering type localities. Confusion about the location of type localities can be avoided simply by using explicit geographic descriptors (political or physical).

COMPARISONS WITH OTHER SPECIES.—Fifteen other species of *Stenocercus* (sensu Fritts, 1974) have an inconspicuous posthumeral pocket (Type 1-2) and a moderately- to well-developed postfemoral pocket (Types 3 or 5): *boettgeri*, *cupreus*, *empetrus*, *formosus*, *guentheri*, *humeralis*, *ivitus*, *nigromaculatus*, *nubicola*, *ochoai*, *orientalis*, *simonsii*, *trachycephalus*, *variabilis*, and *varius*. *Stenocercus imitator* can be distinguished from all of these by the combination of features listed in the characterization, particularly the presence of a prominent projecting vertebral crest in males (crest lacking or non-projecting in

boettgeri, cupreus, empetrus, ivitus, orientalis, simonsi, varius), granular scales on the posterior surface of the thighs (imbricate in *formosus, guentheri, nigromaculatus, ochoai, trachycephalus*), extensive folding of the skin on the neck (absent or weak in *guentheri, ivitus, nigromaculatus, trachycephalus*), a high number of midbody scales (low number [< 80] in *cupreus, ivitus, nigromaculatus, ochoai, orientalis, trachycephalus, variabilis*), and the ventral black collar and other features of coloration in males (absent in *boettgeri, cupreus, empetrus, formosus, guentheri, humeralis, nubicola, ochoai, orientalis, simonsi, trachycephalus, variabilis, varius*).

OSTEOLOGY.— Six dry skeletons were available, five males: FMNH 232584 (SVL 100), FMNH 232585 (SVL 83), FMNH 232586 (SVL 90), FMNH 232587 (SVL 100), and FMNH 232588 (SVL 94); and one female: FMNH 232590 (SVL 80); and two cleared and double-stained specimens (ANSP 31739, male, SVL 79; ANSP 31732, female, SVL 71). The nine osteological characters discussed by Etheridge (1966) conform to the "South American pattern" in *Stenocercus imitator*. There are three pairs of sternal ribs, two pairs of xiphisternal ribs (mostly calcified), and two pairs of calcified inscriptional ribs that approach one another closely midventrally. There are no xiphisternal rods. There are only slight rugosities on the dorsal roofing bones of the skull, most on the parietal and posterior part of the frontal; they appear as numerous ridges whose correspondence to the overlying scale pattern is difficult to discern. The region of nasal/frontal contact is well-ossified. The parietal foramen is absent. The superior fossa of the quadrate is variably more open in smaller individuals (FMNH 232585-86, 232590) than in larger ones (FMNH 232584, 232587-88), in which the fossa is constricted dorsally. The tricuspid maxillary teeth are slightly compressed and not flared. Pterygoid teeth are variably present: all dry skeletons and ANSP 31732 have 2-5 teeth on each bone; ANSP 31739 lacks pterygoid teeth.

NATURAL HISTORY OBSERVATIONS.— *Stenocercus imitator* is an abundant lizard in the vicinity of the type locality. Although it appears to be uncommon in the deeply shaded parts of the forest, it is found in more open areas within the forest where breaks in the canopy allow light to hit the ground (Fig. 16). It is common in secondary forests and disturbed habitats (agricultural plantations such as banana and coffee groves) at lower elevations in the vicinity of Monte Seco, along road cuts (Fig. 16), and, at higher elevations (up to 2600m), in scrub forests and open brushy habitats. It is sympatric with *Stenocercus percultus* at lower elevations in the vicinity of the type locality, and at two localities in Piura Department (west of the Abra de Porculla and near Canchaque). At the type locality and near Canchaque it is sympatric with *S. chlorostictus* new species. On the high tableland in the vicinity of the town of Udima (Fig. 25) *Stenocercus imitator* is sympatric with *Stenocercus eunetopsis*.

Most individuals of *Stenocercus imitator* were active on the ground, but frequently used perches of fallen trunks, rock outcrops, or fence rows. Some specimens were taken from vertical rock walls and one individual was observed on a lateral branch of a tree in a banana grove about 4-5m from the ground. When inactive or disturbed they commonly took refuge under surface objects, particularly in cavities under rocks or logs. Less commonly, they used holes in the ground. Around the town of Udima, agaves were common and *Stenocercus imitator* often retreated into the base of these plants.

No attempt was made to comprehensively survey specimens for reproductive activity. At the Río Zaña localities females with enlarged ova (>10mm) were collected only at the beginning of the dry season (11 May - 17 June 1987), but the number of adult females collected during the rainy season (January 1989) was very small. One female (ANSP 31732, SVL 71) collected during the rainy season had ova <2mm in diameter. Gravid females range in SVL from 70-83mm. Six clutches counted included 4 ova or 5 ova (3 clutches each).

Eight specimens (FMNH 232609-16) inferred to be close to hatching size (30-34mm

Fig. 16. Habitats of *Stenocercus imitator*, both from the slope northeast of Monte Seco, Río Zaña, Depto. Cajamarca, Perú, approximately 1600-1700m (see also Fig. 25). Photograph above shows open, degraded habitat along a road. *Stenocercus imitator* was common among boulders and beneath vegetation in this area. Photograph below shows a boulder-strewn trail through a forest. *Stenocercus imitator* were found beneath these boulders, as well as on the ground in the adjacent shaded forest.

SVL) were collected between 20 May and 18 June 1987. No individuals of this size were observed during field work in the rainy season (January 1989). These observations are consistent with those concerning females with enlarged ova, which were present only early in the dry season (see above), although the presence of hatchlings as early as 20 May suggests that egg-laying began before I arrived at the field site (1 May).

Amended description of *Stenocercus simonsi* Boulenger Figs. 17-18

The following features more thoroughly characterize *Stenocercus simonsi* Boulenger (1899) than those provided in the original description or in Fritts (1974), and will aid in distinguishing this species from one described in the following accounts. I have examined the two syntypes and samples of two populations from Girón (Prov. Azuay) and Saraguro (Prov. Loja), Ecuador. Meristic values for these specimens are summarized in Table 5. As noted by Fritts (1974:64-65), the two latter population samples differ significantly in several standard meristic characters.

DESCRIPTION.— *Head* (Figs. 17-18). Dorsal head scales small, juxtaposed, smooth; often densely covered with scale organs, especially anteriorly. Internasals 4, but irregular in shape and arrangement. No distinct parietals, interparietal, or postparietals; posterior head scales small, irregular. Parietal eye not visible. Two canthals (occasionally a small third one just anterior to eye), separated from nasals by tiny scales. Supraorbital semicircles irregular, in contact via 1-3 scales, occasionally partially separated by a broken row of tiny scales intercalated between them. No enlarged supraoculars; or, if one row appears somewhat enlarged, then the scales are generally less than twice the size of scales in adjacent rows (the type description states: "Middle supraoculars broader than long. . . ," but this is true only in some of the specimens available). No projecting blade-like or strongly keeled angulate temporals. Lateral temporal scales small, juxtaposed, smooth. Preauricular fringe reduced (2-4 scales). Gulars smooth. Two or three rows of sublabials between the infralabials and the postmental series at a point ventral to the midpoint of the eye.

Neck and body. Dorsal scales of neck very small, almost coarsely granular. Lateral neck scales more finely granular. Dorsal body scales imbricate, moderately keeled, but not mucronate, grading gradually into small, somewhat coarsely granular lateral scales. Vertebral scale row keeled and distinctly larger than adjacent rows (occasionally becoming somewhat indistinct posteriorly). Ventrals smooth, about the same size as middorsals.

Neck folds and mite pockets. Neck region strongly folded. Complete complement of dorsolateral, supra-auricular, antehumeral, gular, antegular, oblique neck, longitudinal, and postauricular folds. Gular folds of opposite sides separated by about 5 scales midventrally. Antegular fold particularly well-developed, and positioned halfway between the posterior border of the ear and the gular fold, or somewhat closer to the gular fold. Distinct mite pockets present under the antehumeral fold (usually at or above the level of the dorsal edge of the forelimb) of most adult males examined (present in KU 134157, 134162-63; absent in KU 134168), and some adult females (KU 134158, 134161, 134164). Antehumeral mite pockets absent or indistinct in other females and subadults. They were not present in one syntype of *simonsi*, BMNH 1946.8.11.73, but this specimen is a subadult with poorly developed neck folds; this feature was not discovered until after my examination of the other, larger, syntype, so consequently was not noted in that specimen. Occasionally (e.g., KU 134164) a few mites were observed under other neck folds. These mite pockets have apparently not been reported previously in *Stenocercus*. They are less well-developed than the mite pockets among the neck folds in members of the *Tropidurus torquatus* group (Rodrigues 1987) and are not obviously present in all individuals of *S. simonsi*. In members of the *T. torquatus* group, the neck

Table 5. Variation for standard meristic and mensural features for the syntypes and two population samples of *Stenocercus simonsi*. For the samples from Girón and Saraguro, Ecuador, sample sizes (N) are 8 and 10, respectively, unless otherwise indicated. For scale counts, range or range followed by mean and standard deviation are given.

	Syntypes: Oña, Prov. Azuay			
	BMNH 1946.8.11.73 ? male	BMNH 1946.8.11.74 male	Girón Prov. Azuay	Saraguro Prov. Loja
Midbody scales	101	90	79-102 91.13 ± 7.7	88-102 96.4 ± 5.06
Vertebral scales	70	72	59-80 68.38 ± 7.9	68-98 78.6 ± 9.9
Paravertebral scales	111	109	94-120 102.13 ± 11.1	100-120 110.7 ± 6.16
Gular scales	—	53	36-49 44.38 ± 4.4	51-57 52.8 ± 2.2
Internasals	4	4	4	4
Supraoculars	—	7-9	6-8	6-8
Lamellae, 4th Finger	28	25	24-27 25.62 ± 1.3	25-28 26.5 ± 0.97
Lamellae, 4th Toe	35	33	28-31 29.0 ± 1.07	30-37 32.3 ± 2.06
Maximum SVL, Males Females	55	70	88 79	80 72
Tail L/Total L	0.65	—	0.59 (N=1)	0.62-0.63 (N=4)

pockets consist of a distinct (usually deep) pouch, whereas in *S. simonsi*, the pockets take the form of a thinning of the scales (sometimes to the point of having bare skin) along the furrow of the antehumeral fold, occasionally accompanied by a slight depression. It would be desirable to more clearly delineate the forms of neck mite pockets and evaluate their variation more carefully. In addition to *S. simonsi* I found antehumeral mite pockets in several other species (see species account for *S. carrioni* and the discussion of relationships).

Tail. Tail rounded proximally; moderately compressed distally. Caudal scales large, strongly keeled dorsally, laterally, and ventrally, and extremely spinose. Boulenger's (1899:454) statement that the tail in *simonsi* is "nearly twice the length of the body" applies only to one of the syntypes with a complete tail (BMNH 1946.8.11.73, subadult; SVL 55, Tail 103; Tail L/Total L = 0.65). All of the other specimens I examined have shorter tails (Tail L/Total L 0.59-0.63).

Limbs. Dorsal scales of forelimbs imbricate,

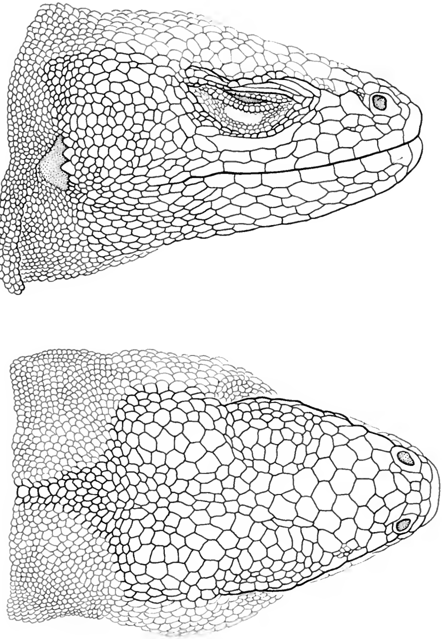

Fig. 17. *Stenocercus simonsi* (male, SVL 88, KU 134163). Dorsal and lateral (left side, reversed) views of head. Ecuador: Prov. Azuay: Giron, 2240-2500m. Drawn by L. Meszoly, used with permission of E. E. Williams.

weakly keeled or smooth. Supradigitals smooth. Ventral scales of proximal forelimb granular, smooth; of distal forelimb imbricate, smooth. Scales on the posterior surface of thigh granular. Dorsal scales of hindlimb imbricate, strongly keeled; ventral scales of hind limb imbricate, smooth.

Dermal pockets. Posthumeral pocket absent (Type 1). Postfemoral pocket moderately developed (Type 3).

Pattern and Sexual Dimorphism (preserved specimens only). Little or no sexual dimorphism in coloration or pattern (males are larger and somewhat more robust [e.g., broader heads] than females). Dorsum with bold black bar in front of forelimb that sometimes meets the corresponding one from the opposite side middorsally. Similar series of dorsal bars on body (1-4) that vary in distinctness. Head scales brown bordered with black. Light bar extending from below the eye, across the dorsal margin of the ear to the black antehumeral bar,

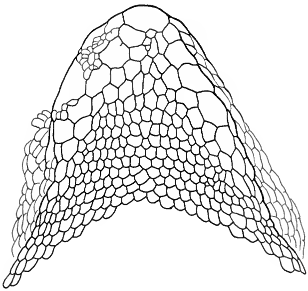

Fig. 18. *Stenocercus simonsi* (male, SVL 88, KU 134163). Ventral view of head. Drawn by L. Meszoly, used with permission of E. E. Williams.

sometimes continuing posteriorly onto the anterior part of the body. Tail banded with black and yellowish brown. Limbs irregularly barred. Throat grayish white to gray with scattered dark gray punctations. Belly grayish white with gray punctations laterally. Flanks grayish with scattered light and dark spots.

DISTRIBUTION (Fig. 5).— *Stenocercus simonsi* is known only from three localities within the drainage of the upper Río Jubones system of southern Ecuador (Prov. Loja and Azuay; the type locality, Oña, is very close to the town of Saraguro, from which a series is available). Boulenger (1900:183), without citing specimens, reported *Stenocercus simonsi* from "Baños, Cajamarca" [Perú], the type locality of *S. melanopygus*. This locality, referred to on some contemporary maps as "Los Baños" or "Los Baños del Inca," is about 5 km east of the city of Cajamarca. At my request, A. F. Stimson located five specimens in the collections of The Natural History Museum (London) to which Boulenger apparently was referring when he noted the presence of *simonsi* there. (Stimson, *in litt.*, notes that BMNH correspondence indicates that the correct locality for these five specimens is probably the nearby city, Cajamarca, rather than Baños). I have examined three of these (BMNH 1900.3.30.1-3) and all are referable to *Stenocercus empetrus* Fritts, which is well-known from the basin surrounding the city of Cajamarca (see Fig. 5); the other two specimens in this series (BMNH 1900.3.30.4-5) were examined for me by C. J. McCarthy and determined also to be *empetrus*. Thus, *S. simonsi* is not known from localities outside the valley of the Río Jubones, Azuay and Loja provinces, Ecuador (Fig. 5).

Amended description of *Stenocercus carrioni* Parker
Figs. 19-20, 27

The following description will augment information in Parker (1934) and Fritts (1974), and aid in distinguishing *Stenocercus carrioni* from species described below. Meristic and some other features of *S. carrioni* are summarized in Table 1. My amended description is based on examination of 20 specimens from the known localities on the Pacific versant of southwestern Ecuador, as well as the holotype (see Distribution).

DESCRIPTION.—*Head* (Figs. 19-20). Head scales small, non-protuberant, juxtaposed, smooth or slightly wrinkled; often densely covered with scale organs especially anteriorly and in the loreal region, on the supra- and infralabials, sublabials, and anterior postmentals (scale organs sparse on the type). Internasals 4, but irregular in shape and pattern. Two canthals anterior to the superciliary series. One row of supraoculars variably enlarged; scales sometimes only somewhat larger than those in adjacent rows, and sometimes 2 or 3 times as large. Enlarged supraoculars separated from the supraorbital semicircles by a single, partially doubled, or (rarely) double row of small scales. Supraorbital semicircles in contact, generally via two pairs of scales. No distinct parietals, interparietals, or postparietals. Parietal eye not visible. Lateral temporal scales small, juxtaposed, appearing coarsely granular. Gulars smooth. Often 3 rows of sublabials between infralabials and postmental series at a point

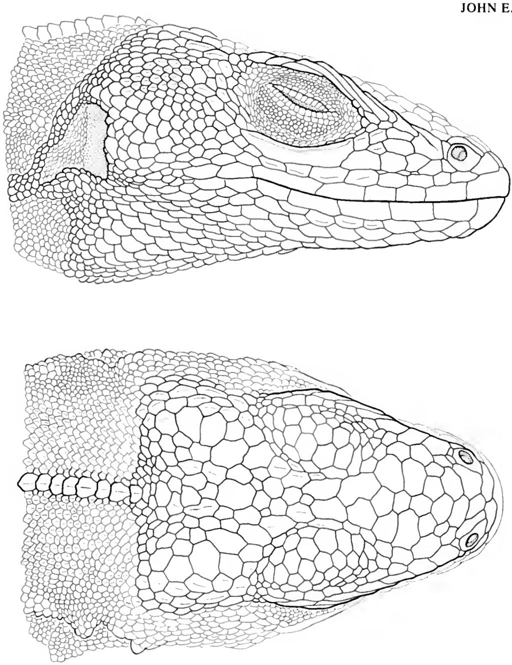

Fig. 19. *Stenocercus carrioni* (female, SVL 67, MCZ 93589). Dorsal and lateral (left side, reversed) views of head. Ecuador: Prov. Loja: 10 km N Celica, 1900 m. The specimen is damaged above the left eye, hence the irregularity in head scales in this area. Drawn by L. Meszoly, used with permission of E. E. Williams.

ventral to eye (sometimes 2 rows, or 2 plus a partial row).

Neck and body. Dorsal neck scales small, keeled, imbricate or subimbricate (in some individuals having a raised, nobby appearance). Lateral neck scales finely granular. Vertebral row keeled and larger than paradorsals on neck and anterior body, becoming indistinct posteriorly; no projecting crest in either sex. Paradorsals imbricate, keeled, but not mucronate. Lateral scales of body granular in axillary region; weakly imbricate and smooth, or having a nobby appearance, posteriorly. Ventrals imbricate, smooth, non-mucronate, subequal to or slightly smaller than paradorsals. Preauricular fringe reduced to 1-3 scales, sometimes barely evident.

Neck folds and mite pockets. Neck region strongly folded, with complete complement of dorsolateral, supra-auricular, antehumeral, gular, longitudinal, oblique neck, antegular, and postauricular folds. Usually a mite pocket is present under the dorsal edge of antegular fold, and consists of a bare patch of skin sometimes

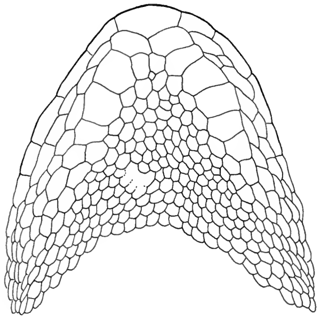

Fig. 20. *Stenocercus carrioni* (female, SVL 67, MCZ 93589). Ventral view of head. Drawn by L. Meszoly, used with permission of E. E. Williams.

accompanied by a slight depression (see comments in the account for *S. simonsi*).

Tail. Tail relatively short (56%-61% of total length). Rounded to slightly compressed. Caudal scales large, strongly keeled dorsally, laterally, and ventrally, and spinose. The alternating large and small whorls mentioned by Fritts (1974: 42) as characteristic of this species are most evident distally and not apparent proximally.

Limbs. Dorsal scales of fore- and hindlimbs imbricate, strongly keeled. Dorsal scales of hand weakly keeled. Supradigitals of hand smooth. Dorsal scales of foot and supradigitals of hind foot strongly keeled. Scales on posterior surface of thigh granular.

Dermal pockets. Posthumeral pocket absent or weakly developed (Type 1 or 2). Postfemoral pocket moderately developed (Type 3).

Pattern (preserved specimens only). The pattern on the holotype (Fig. 27; BMNH 1946.8.11.83; described by Parker 1934) is by far the most distinct of the specimens I examined. I detected no obvious sexual dimorphism. The ground color of the type is greenish gray (greenish brown fide Parker); otherwise the color of preserved specimens is medium to dark grayish brown. There are large, paired, irregular, dark brown paravertebral blotches (5 from above the forelimbs to above the hindlimbs; an additional pair on the neck) on several specimens (e.g., AMNH 18308, 22185; MCZ 93589; BMNH 1946.8.11.83). The median posterior dorsal zigzag stripe mentioned by Parker (1934) is present on the type but not evident in other specimens. A light streak from beneath the eye to the sides of the neck is evident in many specimens, particularly under alcohol (cf. Parker 1934); it passes dorsal to the ear and extends to the anterior part of the body on some specimens. The tail bears indistinct dark dorsal blotches in some specimens (especially evident in the type, Fig. 27). The throat is gray to dark gray, and the belly grayish to brownish gray. Underside of the tail usually lighter than belly color.

Sexual dimorphism and sexual maturity. The largest males are somewhat larger and have slightly more massive heads than the largest females. No prominent sexual dimorphism in pattern was noted among the specimens examined. However, as noted above, few of the specimens examined retained much of the original pattern. The male and female showing most evidence of pattern, BMNH 1946.8.11.83 (holotype) and MCZ 93589, respectively, show no strong differences in pattern. Two females, MCZ 93589 (SVL 67; collected 22 August 1965) and MCZ 133220 (SVL 60; collected between 14 August and 20 September 1921; Chapman 1926: 16, 20), had enlarged ova (> 10mm).

Comments on the Holotype (BMNH 1946.8.11.83, male; Fig. 27). My observations on the holotype of *S. carrioni* generally confirm those of Parker (1934). The interorbital scales of this specimen are small and highly irregular (supraorbital semicircles interrupted), and the keels on the dorsal scales of the body and limbs are weaker than in many of the other specimens examined. The type has well-developed mite pockets underneath the dorsal edge of the antehumeral fold, as do many other specimens. The coloration and the pattern of blotches (see above) described by Parker (1934) are still evident. Scale counts for the type are as follows:

Midbody, 90 ("about 85" according to Parker); Vertebrals, 69; Paravertebrals, 81; Internasals, 4; Supraoculars, 5-6; Subdigital lamellae on the fourth finger, 25; Subdigital lamellae on the fourth toe, 27.

DISTRIBUTION.— As Fritts (1974:42) noted, although the holotype of *Stenocercus carrioni* Parker (1934) was stated to be from Zamora, Ecuador (Prov. Zamora-Chinchipe), a town on the Amazonian slopes, all other specimens come from the Pacific versant in the vicinity of the towns of Celica and Alamor (Loja Province) and adjacent parts of El Oro province in southwestern Ecuador (Fig. 5).

Direct comparison of the type of *Stenocercus carrioni* with specimens from western Ecuador shows that they are similar in all essential respects. The type is still the only specimen of *carrioni* presumably from Zamora, but there is nothing in correspondence between Parker and Carrion in the BMNH archives (letter from Parker to Carrion, 29 June 1933) or in the BMNH ledgers for Carrion's collection that suggests a reason to question the locality (but see Fritts 1974:42 for discussion of other Carrion specimens that seem similarly misplaced). All of the AMNH specimens of *carrioni* from the vicinity of Alamor and Celica were collected by G. H. H. Tate of AMNH's mammal department during the Ecuador expeditions of that museum (Chapman 1926); although AMNH personnel (but not Tate) collected in the vicinity of Zamora, no specimens of *carrioni* resulted. Nevertheless, it is also perhaps worth noting that habitats at Zamora and the vicinity of Alamor and Celica were both originally (prior to deforestation) characterized as transitional between humid tropical and subtropical forests (Chapman 1926). The complexity of terrain and resulting complex distributions of forest types in this region of Ecuador (Chapman 1926) suggest that additional field work will be required to clarify the distribution of *Stenocercus carrioni*. Few ecological data are available for *S. carrioni*. MCZ 93589 is accompanied by a tag which reads: "Habitat: road within humid forest. Shot running in sandy roadbed."

Stenocercus eunetopsis, new species
Figs. 21-22

HOLOTYPE.— FMNH 232537 (field number J. E. Cadle 8087), collected 8 June 1987 approximately 1km SSW Udima, Río de Udima (tributary of Río Zaña), 2500m, Depto. Cajamarca, Perú (Fig. 6).

PARATYPES.— The following specimens, all from the immediate vicinity of the type locality, collected by J. E. Cadle: PERU: DEPTO. CAJAMARCA: Río Zaña, 0.5km N to NW Udima, 2500m: ANSP 31753-54 (adult females), collected 17 January 1989. Río Zaña, 1km S to SE (airline) Udima, 2500-2600m: ANSP 31755-57 (adult males) and 31758-59 (adult females), collected 23 January 1989. Approx. 1km SSW Udima, Río de Udima (tributary of Río Zaña), 2500m: FMNH 232534-36 (adult males); 232538, 232539 (cleared and stained), 232540, all adult females; 232542-44 (adult males), 232545 (adult female), 232546-48 (adult males), 232549 (adult female), 232550 (adult male), 232551 (adult female), 232555 (adult female; skin and associated dry skeleton), 232573 (subadult), 232556 (skin) and associated dry skeleton 232589 (adult male), collected 8 June 1987; and FMNH 232541, 232553-54 (adult males), 232549, 232552 (adult females), collected 20 May 1987.

DISTRIBUTION* (Figs. 5-6).—*Stenocercus eunetopsis* is known only from the vicinity of Udima, Depto. Cajamarca, Perú. The known elevational range is 2450-2600m. A sharp escarpment separates the rolling tableland in which Udima lies from the forested slopes above Monte Seco. *Stenocercus eunetopsis* is not known from the humid forests covering these slopes, nor from the shorter-stature and drier forests at lower elevations west of Monte Seco.

ETYMOLOGY.— The specific epithet is derived from the Greek noun "*euneter*" (gender, masculine) meaning "bedmate" or "spouse," and the suffix "*-opsis*" meaning "having the appearance of." The reference is an allusion to the lack of strong sexual dimorphism in this species.

CHARACTERIZATION.— (1) head scales smooth, non-protuberant; (2) no distinct parietals, interparietal, or postparietals; posterior head scales small, irregular; (3) internasals 3 or 4, occasionally 5; (4) no enlarged supraoculars;

* During field work subsequent to completion of this paper, a specimen of *Stenocercus eunetopsis* was collected from 3 Km by road (Llama to Huambos) N La Colmena, 2640m, Depto. Cajamarca, Perú (J. E. Cadle 10248, in the Museo de Historia Natural de San Marcos, Lima). This extends the known range of the species to the mountains north of the Río Reque, the major river system north of the Río Zaña.

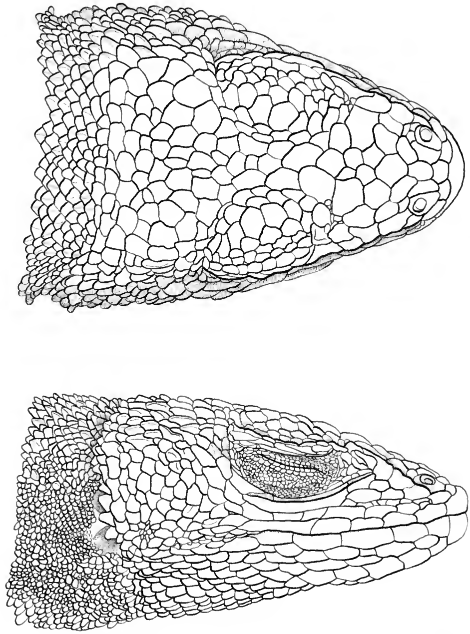

Fig. 21. *Stenocercus eunetopsis* (male, SVL 79, FMNH 232534). Dorsal and lateral views of head. Perú: Depto. Cajamarca: Approx. 1 km SSW Udima, Río de Udima (tributary of Río Zaña), 2500 m. Drawn by G. Bisbee.

(5) two (rarely one) canthals on either side anterior to the superciliaries; (6) no projecting or blade-like angulate temporals; (7) gular scales smooth; (8) parietal eye not visible; (9) relatively complete series of neck folds present, including well-developed antehumeral, gular, dorsolateral, ventrolateral, supra-auricular, longitudinal, and oblique neck folds; weak or, occasionally, moderately-developed antegular fold present; (10) dorsal scales imbricate and keeled, larger than lateral and ventral scales; (11) no projecting vertebral crest; vertebral scales not distinctly larger than other dorsal rows; (12) posthumeral pocket absent or weakly-developed (type 1-2); postfemoral pocket shallow, sometimes with a thickened border that may slightly cover the pocket (type 2-3); mite pocket variably present or absent under the antehumeral fold; (13) scales of posterior thigh granular; (14) tail rounded to slightly compressed; caudal scales extremely spinose; (15) little sexual dimorphism in coloration and pattern; dorsum with a series of black bars, widest middorsally, separated by yellow lines

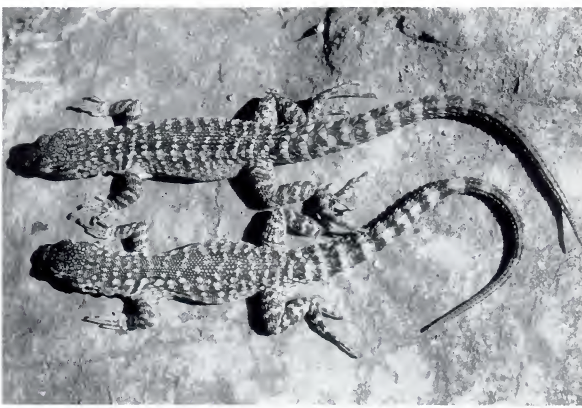

Fig. 22. *Stenocercus eunetopsis*. Above, an individual with indistinct dorsal markings (from the series FMNH 232534-56). Below, FMNH 232541 and FMNH 232553 (both males, SVLs 73 and 71, respectively), showing more distinct dorsal cross bars and antehumeral bar. All from vicinity of the type locality.

(pale yellow to white in preservative); limbs barred similarly; dorsal head scales brown with black border.

DIAGNOSIS.—*Stenocercus eunetopsis* differs from all species of *Ophryoessoides* sensu Fritts (1974) in lacking enlarged posterior head scales and keeled ventral scales, and in having a relatively more rounded tail. It can be distinguished from all other species of *Stenocercus* by having the combination of (1) absent or weakly-developed posthumeral pockets (Type 1-2), and shallow postfemoral pocket (Type 2-3); (2) well-developed neck folds; (3) vertebral scales not distinctly larger than paradorsals, and without projecting vertebral crest; (4) granular scales on the posterior surface of the thigh; (5) extremely spinose caudal scales; (6) imbricate, strongly keeled dorsal scales on neck and body, weakly imbricate lateral body scales; (7) little sexual dimorphism; and (8) antegular fold at a level just posterior to the ear.

DATA ON THE HOLOTYPE.— Snout-vent length, 82. Tail Length, 160. Total length, 242. Midbody scales, 69. Gulars, 37. Internasals, 3. Subdigital Lamellae on 4th finger and toe, 26 and 34, respectively.

DESCRIPTION.— *Head* (Fig. 21). Dorsal head scales small, non-protuberant, juxtaposed, and smooth (but often with many scale organs, giving a highly pitted appearance). In some individuals the posterior head scales are slightly rugose. Rostral narrow, in contact with the first supralabials, first lorilabials, and three postrostral scales. Median postrostral polygonal; lateral postrostrals wider than long. Internasals 3 (10 individuals), 4 (18 individuals), or 5 (1 individual). Nasals separated from the supralabials and rostral by lorilabials and postrostrals. Two canthals anterior to superciliary series, the anterior one usually separated from the nasal by a row of tiny scales (occasionally nasal and anterior canthal in contact). Four or five elongate superciliaries overlapping posteriorly, followed by two or three shorter ones that are juxtaposed or narrowly overlapping in the reverse direction. No distinctly enlarged supraoculars, all of which are smooth. Supraorbital semicircles very irregular; usually in contact via one or (rarely) two scales on the anteromedial edge of the orbits; occasionally in contact via a single undivided anteromedial scale that is part of the semicircle series on each side; occasionally the semicircles are separated by a median row of small scales. No distinct parietals, interparietals, or postparietals; no posterior head scales are consistently and distinctly larger than others. Parietal eye not visible. Lateral temporal scales small, smooth or weakly keeled, and either juxtaposed or weakly imbricate. Ventral head scales all smooth. Mental in contact with the first infralabials and the first pair of postmentals, which are followed by a variable number (3-7) of large postmentals. First pair of postmentals in contact medially and, on each side, with the first infralabial and (usually) the first sublabial. All other postmentals separated by small gular scales. One row (occasionally a partial second row) of sublabials between the infralabials and the postmental row.

Neck and body. Dorsal and dorsolateral scales of the neck and body keeled, larger than lateral and ventral scales. Lateral neck and body scales very small, appearing granular in neck, shoulder, and groin regions; weakly imbricate on the body. Some of the more dorsal of the small lateral body scales are weakly keeled; otherwise they are smooth. Ventral scales smooth, with squarish or obtuse posterior borders. Vertebral scale row not distinctly larger than other dorsal rows, and there is no projecting crest. Auricular fringe reduced (2-4 scales); tympanum well-recessed. Posttympanic scales coarsely granular.

Neck folds and mite pockets. A relatively complete series of neck folds is present. Well-developed antehumeral fold present, continuing onto ventral scales of the lateral portion of the pectoral region as a gular fold, which is interrupted medially. A weak (sometimes moderately-developed) antegular fold present, widely separated from the gular fold. A dorsolateral fold on the body (extending 1/3 to 1/2 the body length) continues anteriorly as a supra-auricular fold, which ends at the posterodorsal edge of the ear opening. Longitu-

dinal neck fold and postauricular fold well-developed. Oblique neck fold present, merging with the antegular fold, and then usually continuing anteriorly a short distance to end on the ventrolateral surface of the throat. A weakly- to moderately-developed rictal fold usually present (but limited in extent to the area immediately ventral and anteroventral to the ear). Rictal fold usually extends along the posteroventral edge of the ear, and is sometimes (e.g., FMNH 232540, 232547) continued as a fold extending posteriorly and dorsally toward the supra-auricular fold; in such cases there is the appearance of a supernumerary oblique neck fold anterior to the "normal" one. A ventrolateral body fold is indicated in some individuals.

Shallow mite pocket under dorsal edge of antehumeral fold, comprising a bare patch of skin of somewhat variable size. In FMNH 232535 (male), for example, it is 1/3 - 1/2 the length of the fold, whereas in FMNH 232540, 232549, and 232552 (female and two subadults, respectively), it is much smaller; a distinct pocket is apparently absent in FMNH 232553, 232541, 232547 (males), although the scales are very small and the skin is only weakly keratinized in this region. One of these individuals (FMNH 232547) has concentrations of mites under the longitudinal neck fold.

Tail (Fig. 22). The tail is rounded proximally and somewhat compressed distally. Dorsal caudal scales very large, strongly keeled, and with large projecting spines. The caudal whorls are subequal in size. Alternate caudal scales rows tend to be black and brown, respectively. Ventral caudal scales, except for a postanal series, strongly keeled and mucronate.

Limbs. Dorsal scales of the forelimbs moderately keeled, not mucronate; those of the hindlimbs strongly keeled and mucronate. Ventral scales of limbs smooth, imbricate. Scales on the posterior surface of thigh granular. Supradigitals mostly smooth, although some scales, especially proximally, are keeled. Scales of palmar and plantar surfaces strongly unicarinate. Subdigitals multicarinate.

Dermal pockets. Posthumeral pocket Type 1 or 2, consisting of, at most, 1-2 wrinkles in the skin, without apparent modification of the skin surface. Where mites occurred in concentration, the skin was thickened. The postfemoral pocket is Type 2 or 3, consisting of a scaleless patch of thickened skin (extending from the posterodorsal edge of the thigh about half way down; in females, only a small oval of bare skin is present). The patch is bordered dorsally and posteriorly by a fold in the skin, which is covered by granular scales, and which may form a shallow pocket.

Pattern (Fig. 22). Little sexual dimorphism evident. Body with series of black bars (sometimes obscure in both sexes), widest middorsally, separated by yellow lines. A black antehumeral bar extending dorsally over the scapular region, occasionally meeting its partner from the other side. Limbs and tail barred with black and yellow/yellowish brown. Throat mottled gray and white. Belly pale yellow in life, grayish white in preservative.

Scale counts and measurements (Table 1). This is a relatively small-scaled species having moderately high scale counts. The tail averages slightly less than twice the body length.

Size and sexual maturity. The largest male (ANSP 31755) has a SVL of 83; the largest female (FMNH 232538) has a SVL of 74. Because subadults and adults of this species are similar in coloration and pattern, there are no obvious external features to indicate the onset of sexual maturity. The smallest gravid female (FMNH 232552) has a SVL of 60.

Sexual dimorphism. Adult males are larger than females and have a more bulbous temporal region.

COLORATION.— *Coloration in Life*. There are no obvious differences in coloration of males and females, although females tend to have less distinct markings. The following description is based on detailed notes for an adult male, FMNH 232541 (SVL 73; see Fig. 22). Middorsally, the body bears transverse black bars (nine between the limb insertions) separated by interrupted bright yellow lines, which are one scale wide at most. Laterally, these yellow lines broaden to form a series of dorsolateral irregular yellow blotches. The dorsal

black bars become narrower laterally and form a vertical series along the flanks. They fade gradually to the ventral coloration. In some individuals of both sexes the black dorsal and lateral bars are obscure. Just in front of the forelimb insertions there is a distinct black bar continuous with the middorsal bar; on the neck in front of this are two middorsal black bars that do not extend onto the side of the neck. The dorsal head scales are dirty yellowish or brownish, each with a black border. There is a pale yellow bar from behind to above the tympanum. The dorsal surfaces of the forelimbs are barred with black and yellow; the hind limbs are barred with black and pale yellow/brownish. Dorsal surface of the tail is barred with black and yellowish brown. The throat is mottled with gray and white. The pectoral region and belly are pale yellow, becoming more intense in the posterior belly and pelvic area. The ventral surface of the tail base is pale yellow; more distally it is dirty yellow or brownish with vague indications of banding. The ventral surface of the limbs is dull yellow or whitish.

Coloration in Preservative. The yellow pigment is lost in preservative leaving the scales either whitish (as on the dorsum and venter) or brownish (as on the tail). Otherwise, distinctive features of the pattern remain evident. Scales in which the stratum corneum is lost become grayish white.

COMPARISONS.— *General Comparisons.* Few species of *Stenocercus* have caudal scales that are as large and spiny as those of *S. eunetopsis*. *Stenocercus roseiventris* and *S. marmoratus* from the Amazonian versant of Perú and Bolivia have strongly spinose tails, but both have imbricate, keeled scales on the posterior surface of the thigh (granular in *S. eunetopsis*). In *roseiventris* the dorsal and lateral scales of the tail, except for the middorsal row, are not keeled for most of their length; the tail spines in *roseiventris* are stout, and project more or less vertically from the scale surface; the ventral caudal scales in *roseiventris* are not, or only weakly, keeled. In *eunetopsis* the dorsal, lateral, and ventral caudal scales are strongly keeled for most of their length, and the spines (less robust than in *roseiventris*) are extensions of the keel posteriorly from each scale. *S. marmoratus* differs from *eunetopsis*, in addition, in having fewer midbody scales than *S. eunetopsis* (43-54 [Fritts 1974] versus 60-80, respectively). *Stenocercus crassicaudatus*, also of Amazonian Perú and Bolivia, has a somewhat spinose tail, more midbody scales (89-119; Fritts 1974), and more subdigital lamellae on the fourth finger (30-37) than *S. eunetopsis*; it also has granular scales on the lateral surface of the body (weakly imbricate in *eunetopsis*). *Stenocercus carrioni* of southwestern Ecuador (see Fig. 27) is similar in having very spinose caudal scales (though still not as large or spinose as in *eunetopsis*), but it differs as follows (characters of *eunetopsis* in parentheses; see also amended description of *carrioni* presented above): *carrioni* is a somewhat smaller species, males to SVL 74, females to SVL 69 (83 and 74, respectively); has a shorter tail, 56%-61% of total length (64%-66%); has a distinctly enlarged vertebral scale row on the neck and at least the anterior part of the body (not differentially enlarged); has very small, somewhat coarsely granular scales in the temporal region (polygonal, juxtaposed, larger); and usually three rows of sublabials between the infralabials and the postmental series at a point ventral to the midpoint of the eye (two rows only).

Two other species, *Stenocercus simonsi* and *S. empetrus*, are treated in greater detail because of strong morphological similarities to *eunetopsis* (*simonsi*) or geographic proximity combined with detailed morphological resemblance in some aspects (*empetrus*).

Comparisons with Stenocercus simonsi *Boulenger, 1899* (Figs. 17-18, 21-22). *Stenocercus simonsi* is the species most similar in overall morphology to *eunetopsis*, and I considered the possibility that the available population samples of both represent a single, rather variable species. Hence, I summarize variation within *simonsi* and compare this species to *eunetopsis* in detail. The geographically closest localities for *simonsi* and *eunetopsis* (Saraguro, Prov. Loja, Ecuador for *simonsi*, and the type locality for *eunetopsis*) are about 360km

apart on the western slopes of the Cordillera Occidental, and are separated by several large drainage systems: the Río Catamayo-Río Santa Ana-Río Calvas system of southern Ecuador, and the Río Quiroz, Río Piura, and Río Reque systems of northern Perú (Fig. 5). My conclusion that the specimens from the Río Zaña are specifically distinct from *simonsi* considers the absence of known intermediate populations (despite a fair number of specimens of *Stenocercus* from southern Ecuador, and [many fewer] from northern Perú) and consistent morphological differences among the samples available. Most standard scale counts for *simonsi* are similar to those for *eunetopsis* (see Tables 1 and 5), but *simonsi* averages about 20 more midbody scales and about 2 more supraoculars than *eunetopsis*.

In addition, there are some qualitative differences between *simonsi* and *eunetopsis*. In *eunetopsis* the dorsal scales of the neck are imbricate and strongly keeled (coarsely granular in *simonsi*), and the dorsal scales of the body are strongly keeled (moderately so in *simonsi*). *Stenocercus simonsi* has a continuous morphologically distinct vertebral scale row that is larger and more strongly keeled than any of the paradorsal rows. In *eunetopsis* the scales of the vertebral row are about equal in size and keeling to those of adjacent paradorsal rows. The paradorsals in *eunetopsis* are larger and more strongly keeled than in comparably-sized specimens of *simonsi* (this is reflected in the higher midbody counts for *simonsi*). The keeling and spine development on caudal scales of *eunetopsis* and *simonsi* are very similar. In both species all caudal scales, including ventral ones, are strongly keeled for most of the length of each scale (compare *S. roseiventris*, as noted above [General Comparisons]).

Stenocercus simonsi seems to be a somewhat more robust animal than is *S. eunetopsis*, but this difference is subtle and difficult to quantify given the differences in preservation of specimens. The largest specimens of both species are nearly the same size (83 and 88 mm; Table 1), but larger specimens of *simonsi* appear to have a more massive head and neck region, and they are somewhat broader across the temporal region than *eunetopsis* of similar size.

Stenocercus simonsi has a very prominent antegular fold that is much deeper than the antegular fold of *eunetopsis*; in *simonsi* the antegular fold has 6 or more minute scale rows within the fold, compared to 1-3 rows in *eunetopsis*. The distance between the antegular and gular folds of *simonsi* is much less than the comparable distance in *eunetopsis*. As a somewhat quantitative way of visualizing this difference, I measured the distance between the antegular and gular folds (midventrally, between the antegular fold and a line drawn between the ventral ends of the gular folds, which are not complete ventrally in *simonsi* or *eunetopsis*), and divided this measure by the distance between the gular fold and the anteroventral margin of the ear. In *simonsi*, this ratio averaged 0.47 ± 0.08 (N=7; range 0.37-0.64), whereas in *eunetopsis* this ratio averaged 0.69 ± 0.06 (N=9; range 0.60-0.78). Another indication of this difference is the position of the antegular fold relative to the posterior margin of the ear and the gular fold: in *simonsi*, the antegular fold is about midway between these two points, or somewhat closer to the gular fold; in *eunetopsis* the antegular fold is positioned at a level just posterior to the ear.

The presence of shallow mite pockets under the antehumeral folds is shared by some specimens of both *eunetopsis* and *simonsi* (and by some other species: most specimens of *carrioni* examined [see amended description above], and some *cupreus* [FMNH 5613, 16178] and *chrysopygus* [FMNH 81507]). These pockets are more consistently present in *eunetopsis* (see Description), but were observed in specimens of both sexes of *simonsi* from Girón, Ecuador (KU 134157-58, 134161, 134163-64), and absent in specimens of both sexes from Girón and Saraguro, Ecuador (KU 134160, 134165-69). The possibly unusual nature of this feature in *Stenocercus*, but its variable presence in both *simonsi* and *eunetopsis*, is considered potential evidence for a close relationship of these species (See Discussion: Phylogenetic Relationships).

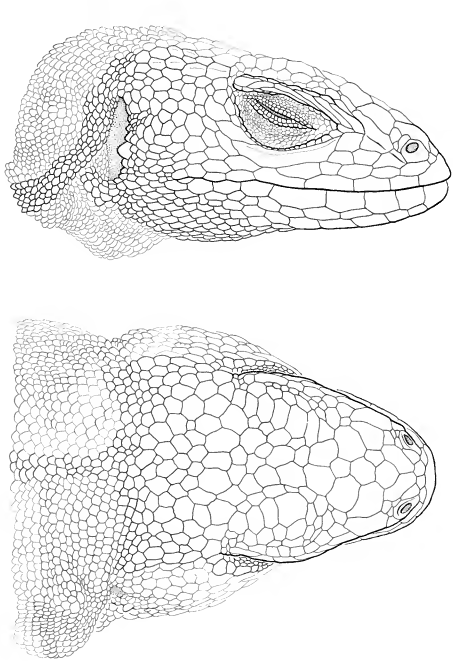

Fig. 23. *Stenocercus empetrus* (female, SVL 78,·MCZ 8084). Dorsal (top) and lateral (bottom; left side, reversed) views of head. Perú: Depto. Cajamarca: Baños. Drawn by L. Meszoly, used with permission of E. E. Williams.

Comparisons with Stenocercus *empetrus Fritts, 1972* (Figs. 21, 23-24). Finally, *Stenocercus empetrus* is geographically proximate to and, in some respects, is similar to *S. eunetopsis*. Notably, both species show little sexual dimorphism in coloration or other features (development of dorsal crest, morphology of the tail), and the primary dorsal pattern in both species consists of some mixture of black or brown scales, and yellow scales. Both are highland species in geographic proximity on opposite sides of the Cordillera Occidental (Fig. 5). *Stenocercus empetrus* is known from 2600-3100m at localities mainly east of the continental divide in the departments of Cajamarca and La Libertad. Its distribution approaches that of *S. eunetopsis* in the vicinity of Celendín and Cajamarca (both in Cajamarca Department), approximately 100km and 75km to the east and southeast, respectively (Fig. 5).

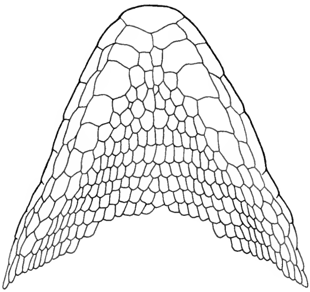

Fig. 24. *Stenocercus empetrus* (female, SVL 78, MCZ 8084). Ventral view of head. Drawn by L. Meszoly, used with permission of E. E. Williams.

The only known locality for *Stenocercus empetrus* on the Pacific versant, near Otuzco (La Libertad department; FMNH 5708), is approximately 135km SSE of the type locality for *S. eunetopsis* (see comments on this locality below).

Some variation in coloration and the extent of sexual dimorphism, presently inadequately understood, occurs among populations of *Stenocercus empetrus* (Fritts 1972). However, as presently defined (Fritts, 1972, 1974; supplemented with personal observations), *S. empetrus* and *S. eunetopsis* are easily distinguished by the following features (characteristics of *S. empetrus* in parentheses): dorsal neck scales imbricate, keeled, and distinctly set off from lateral neck scales, which are granular (dorsal neck scales coarsely granular, smooth, grading gradually into lateral neck scales); lateral body scales finely imbricate and abruptly set off from dorsals (lateral body scales granular); caudal scales large, very spinose, and with a strongly projecting keel (caudal scales smaller, not as projecting; compare Fig. 22 and Fritts 1974:Fig. 39); body scales moderate in size, 60-80 around midbody (smaller, 87-115 around midbody); alternating dark and light bands on dorsum of body and, especially, the tail (dorsal body and tail pattern generally dark with light flecks and spots not forming bands); venter mostly yellowish to whitish, with some gray mottling on throat (yellow to orange- yellow with bold black reticulations).

The difference in size and projection of the caudal scales is the most striking feature distinguishing *S. eunetopsis* and *S. empetrus*, and is reflected in the number of scales around the base of the tail; these range from 17-24 (mean $= 21.1 \pm 2.0$; N = 29) in *S. eunetopsis* and 23-36 (mean $= 27.8 \pm 2.9$; N = 24) in *S. empetrus*. In addition to these differences *S. empetrus* reaches a larger size (males to SVL 101 and females to SVL 89, respectively) than *S. eunetopsis*, is a generally more robust animal with a more bulbous temporal region, and has a shorter tail (51-61% of total length, compared to 64-66% in *S. eunetopsis*).

Comments on the distribution of Stenocercus empetrus on the Pacific versant of the Andes. Fritts (1972, 1974) reported *Stenocercus empetrus* from intermediate elevations of the Pacific drainage on the basis of a single specimen (FMNH 5708) from "Otuzco" (Depto. La Libertad, Perú). This specimen was obtained by W. H. Osgood and M. P. Anderson during a Field Museum of Natural History expedition to northern Perú, primarily for the collection of mammals and birds. Although the FMNH catalog records "Otuzco" as the locality for FMNH 5708, reference to a published report of the expedition makes clear that the specimen actually came from higher elevations to the north: "The locality to which this phrase ['mountains near Otuzco'] refers is near the top of the divide between Otuzco and the Chicama drainage but on the Chicama side overlooking the canyon of Llagueda. Altitude 10,000 ft. ±" (Osgood 1914: 144). Osgood's gazeteer indicates that no specimens were actually collected in Otuzco itself. The mountains he referred to comprise a spur of the Andes rising to more than 4000m and separating the Río Chicama drainage from the Río Moche drainage (cf. Fig. 5). Thus, although technically from Pacific drainages, the "Otuzco" specimen of *S. empetrus* comes

from the mountains (> 3000m) that form a continuous high tableland between the western (Pacific) parts of the Cordillera Occidental and their eastern (Río Marañon, ultimately Amazonian) extensions in this region.

OSTEOLOGY.—Two dry skeletons (FMNH 232555, female, SVL 77 mm; and FMNH 232589, male, SVL 85 mm) and one cleared and double-stained specimen (FMNH 232539, female, SVL 65) were available. For the nine osteological characters discussed by Etheridge (1966) *S. eunetopsis* conforms to the "South American" pattern. There is sculpturing on the parietal, frontals, prefontals, nasals (including anteriorly), and the postorbitals. The sculpturing is most concentrated on either side of the parietal-frontal border, and occurs there as many small irregular rugosities which appear to correspond to the overlying scale pattern (borders between rugosities not discrete). The region of the nasal-frontal contact is well-ossified. On the right side of FMNH 232539 the prefrontal and the dorsal extension of the maxilla are reduced, and replaced by a cartilaginous or fibrous (blue-stained) capsule. The parietal foramen is absent (most specimens) or present (FMNH 232539). The superior fossa of the quadrate is relatively open in both specimens. The tricuspid maxillary teeth are slightly compressed, not flared. Pterygoid teeth are consistently absent; in the male (FMNH 232589) there is a rugosity on each pterygoid in the position where the teeth would be, but its surface is smooth, suggesting that teeth have not simply broken off.

FMNH 232539 shows some unusual features of the rib formula. There are three pairs of sternal ribs and two pairs of xiphisternal ribs (mostly calcified). The last xiphisternal rib on the left side is incomplete near the midline, and is separated by a gap (approximately 1mm) from attachment to the xiphisternum. Xiphisternal rods are absent. A single pair of postxiphisternal inscriptional ribs approach closely on the midline; their tips are bifurcate (more prominently on the right than on the left side). The next pair of dorsal ribs bears short cartilaginous inscriptional ribs (approximately 2.5mm long) which do not extend ventrally. Normally in South American iguanids there are two or more pairs of inscriptional ribs that closely approach one another midventrally (Etheridge 1965), and the first pair of dorsal ribs following the inscriptional ribs is abruptly shorter than the preceding ones. In FMNH 232539, the pair of dorsal ribs bearing the very short inscriptional ribs (i.e., the second pair) is not reduced, but the following pairs of dorsal ribs are, as is usual in iguanids (Etheridge 1965).

NATURAL HISTORY OBSERVATIONS.—*Stenocercus eunetopsis* is known from only a very restricted area near the town of Udima (Figs. 6 and 28). At the crest of the ridge north of Monte Seco, the wet forest is abruptly replaced by disturbed habitats, either open pastureland or a low-canopy (< 5m) scrub forest. Weathered rock outcrops dot the landscape (Fig. 25). The terrain at the top of the ridge is generally rolling hills surrounding a valley in which the town of Udima lies. Streams draining this valley eventually empty into the Río Udima, which flows westward to join the Río Zaña near the town of Espinal, downstream from the Monte Seco area. According to Koepcke (1961) the Udima area was once covered by a mixture of "mesothermic and oligothermic rainforest," now existing in only fragmented patches. As recently as the late 1950s this forest was "nearly unaltered by human activities" (Koepcke 1961:36). This contrasts with the mesothermic and cloud forest habitats (in Koepcke's terminology) characteristic of the slopes north and east of Monte Seco. Thus, the native habitat of *Stenocercus eunetopsis* was perhaps a somewhat drier and more open formation than the slope vegetation, which may account for its apparent absence in the more humid areas.

Stenocercus eunetopsis was collected in relatively open habitats between 2450-2600m, most commonly in areas providing crevices or holes in the soil for retreat (Fig. 25). One such area where most individuals were captured was a road cut consisting of a vertical bank 1-3m high which, during the dry season, was penetrated by numerous deep crevices formed in

Fig. 25. Habitat of *Stenocercus eunetopsis* and of *S. imitator*. Photograph is of the tableland north of the escarpment separating the Río Zaña from the Río Udima between Monte Seco and Udima, Depto. Cajamarca, Perú, approximately 2500m (see Fig. 6). Although now nearly devoid of forests, according to Koepcke (1961: 36) this area was once extensively wooded. *Stenocercus eunetopsis* was found on the ground in open areas with grass cover or bare earth, or areas with a covering of shrubs, and used retreats in the ground or crevices in vertical road cuts. *Stenocercus imitator* was found in areas with boulders or shrub/tree cover, rarely in completely open ground, and usually sought refuge under surface objects, boulder piles, or dense shrubs; occasionally they used crevices in the ground.

the clay-like soil. The lizards were active on the vertical portions of the bank, as well as flatter ground both above and below; crevices within the bank were used as retreats. Some individuals were active on flat terrain in grassland away from rocks, but apparently the ground was penetrated by numerous holes into which they could flee. Although individuals of *S. eunetopsis* were observed around rock outcrops, they did not appear as commonly in this microhabitat as did the sympatric species, *S. imitator*.

At the type locality *Stenocercus eunetopsis* was active during sunny parts of the day, but retreated into holes or crevices in the ground late in the afternoon. They are wary when active, and are most easily obtained by digging

them out of retreats. The largest series of individuals (28) was collected from crevices in the road cut described above from 1630-1800hr, at which time the lizards had already retired for the day. During this time only 6 *S. imitator* were collected by this method, suggesting that this species uses a different kind of retreat (on one occasion, one individual each of *S. eunetopsis* and *S. imitator* was obtained from the same crevice).

During the rainy season (observations 22-24 January 1989) *Stenocercus eunetopsis* is not as apparent as during the dry season (observations May-June 1987). During the rainy season they were active early to mid-morning when the sun was very hot, but with gathering clouds late in the morning they retreated into burrows for the day (late morning cloudiness followed by rain much of the afternoon was typical of the rainy season observation period).

Seven of eight female *S. eunetopsis* collected at the beginning of the dry season (20 May and 8 June 1987) bore enlarged (> 10mm) ova. These females ranged in size from 60-77 mm SVL. A slightly smaller female collected during the same period (FMNH 232549; SVL 58) had ova < 2mm in size. Only one (ANSP 31754; SVL 65) of four females collected during the rainy season (17 and 23 January 1989) had enlarged ova, whereas the other three (SVL range 65-70) contained only small ova. One recent hatchling (FMNH 232573; SVL 32) was collected 8 June 1987. The clutch size for the three specimens determined (FMNH 232539, 232552, 232555, all collected during the dry season, 20 May and 8 June 1987) was two; these specimens span the size range (60-77 mm SVL, respectively) of gravid females.

Stenocercus chlorostictus, new species
Figs. 26-27

HOLOTYPE.— ANSP 31760 (field number J. E. Cadle 9279), an adult male collected 6 September 1988 by Raul Quiroz from El Chorro, a village 1km N (airline) Monte Seco, 1350m, Río Zaña, Departamento de Cajamarca, Perú (Fig. 6).

PARATYPES.— PERÚ: DEPTO. PIURA: about 15km (by road) E Canchaque on Huancabamba road, about 5700ft. [1740 m]: LSUMNS 27231-33 (adult females), SDSU 1535 (adult male), all collected 4-9 December 1974 by Richard Thomas.

DISTRIBUTION (Fig. 5).— Known from northern Perú at the type locality in the valley of the Río Zaña (Depto. Cajamarca) and from the slopes immediately east of Canchaque (Depto. Piura). The known elevations are 1350 m at the former locality and 1740m at the latter. Both localities are on the Pacific versant of the Andes.

ETYMOLOGY.— The specific epithet is an adjective derived from the Greek words "*chloros*," meaning "green" and "*stiktos*," meaning "spotted" or "dappled," and refers to the primarily green dorsum of males in this species, and their light green dorsal spots.

DATA ON THE HOLOTYPE.— Snout-Vent length, 66. Tail length, 94. Total length, 160. Midbody scales, 81. Gulars, 38. Internasals, 4. Subdigital lamellae on 4th finger and toe, 23 and 25, respectively.

CHARACTERIZATION.— (1) dorsal head scales small, non-protuberant, smooth; (2) no distinct parietal, interparietal, or postparietal scales; posterior head scales small, irregular; (3) internasals 4; (4) no enlarged supraoculars; (5) two canthals on either side anterior to the superciliaries; (6) no projecting blade-like angulate temporals; (7) gulars smooth; (8) parietal eye not visible; (9) skin of neck strongly folded, with well-developed supra-auricular, longitudinal, dorsolateral, antehumeral, and gular folds; oblique neck folds, antegular fold, and postauricular folds present; (10) middorsal scales keeled, slightly imbricate, not mucronate; lateral body scales coarsely granular anteriorly, weakly imbricate posteriorly; (11) vertebrals slightly larger and more strongly keeled than adjacent scale rows, but a projecting crest is absent; (12) posthumeral pocket absent (type 1); postfemoral pocket weakly-developed (type 3); (13) scales on posterior surface of thigh granular; (14) tail rounded; dorsal caudal scales large, very strongly keeled,

mucronate, and with moderately projecting spines; (15) dorsal ground color of males green in life, with a bold black collar in front of the forelimb; dorsal ground color of females brown in life, with darker middorsal paired irregular blotches.

DIAGNOSIS.— *Stenocercus chlorostictus* differs from all species of *Ophryoessoides* sensu Fritts (1974) in lacking enlarged posterior head scales and keeled ventral scales, and in having a relatively short, and more rounded tail. It can be distinguished from all other species of *Stenocercus* by having the combination of (1) no posthumeral pocket (Type 1), and shallow postfemoral pocket (Type 3); (2) well-developed neck folds; (3) vertebral scales slightly larger and more strongly-keeled than paradorsals, but without projecting vertebral crest; (4) granular scales on the posterior surface of the thigh; (5) tail rounded and 60% or less of total length, and with enlarged, very stongly keeled caudal scales; (6) strong sexual dichromatism: in life, males primarily green with a bold black antehumeral collar; females brown with paired middorsal irregular blotches.

DESCRIPTION.— *Head* (Fig. 26). Dorsal head scales small, non-protuberant, juxtaposed, and smooth. Dorsal head scales in front of orbits somewhat larger than those posterior to orbits. Rostral small, with smooth or undulating border above; in contact with first supralabial, first lorilabial, and 4-5 small postrostrals. Postrostrals subrectangular or polygonal; lateral ones may be slightly wider than long. Nasals generally separated from rostral and supralabials (in one individual, LSUMNS 27232, nasal barely touches rostral on one side only). Internasals 4, irregular in shape, although the two medial ones are usually narrower anteriorly than posteriorly. Two canthals in front of superciliary series, the anterior one in contact with the nasal, or (the usual condition) separated from it by tiny scales. Four or five elongate superciliaries overlapping posteriorly, followed by 2-3 shorter posterior superciliaries overlapping in the reverse direction. No enlarged supraoculars, all of which are smooth; supraoculars at greatest width of orbit usually 6 (sometimes 5). Supraorbital semicircles in broad contact via two scales on the medial and anteromedial border of the orbit. No distinct frontals, parietals, interparietal, or postparietals. Posterior head scales are small, highly irregular. Dorsal head scales anterior and medial to orbits are somewhat larger than posterior head scales. Parietal eye not visible. Lateral temporal scales small, slightly protuberant or knobby, juxtaposed. Ventral head scales smooth. Mental in contact with first infralabials and first postmentals, which are in contact with each other (Canchaque specimens) or separated by a tiny median scale (holotype). The first pair of postmentals in contact with the first infralabials and the first sublabials. The first postmentals are followed by 3-5 additional enlarged postmentals.

Neck and body. Dorsal and dorsolateral scales of neck and body keeled, slightly imbricate, with rounded or obtuse posterior borders. Lateral neck scales small, coarsely granular. Lateral body scales coarsely granular anteriorly, having a smooth or somewhat knobby appearance, becoming very weakly imbricate (subimbricate), and smooth or weakly keeled posteriorly. Transition from larger dorsolateral scales to smaller lateral scales, and the lateral scales to ventral scales is more or less abrupt. Ventrals smooth, imbricate, subequal to paradorsals, and with squarish posterior borders. The vertebral row is slightly, but distinctly, larger than adjacent scale rows, and is continuous from the nape (holotype) or middle of the neck (Canchaque specimens) to the base of the tail; there is no projecting dorsal crest, but the vertebral row is somewhat more strongly keeled than dorsolateral rows, especially anteriorly. Tympanum moderately recessed. Preauricular fringe very reduced (two scales on each side).

Neck folds. In the holotype the neck folds are obscured because of overinflation of the specimen. These descriptions are based primarily on the paratypes. Well-developed supra-auricular, longitudinal, and dorsolateral folds. Well-developed antehumeral fold extends over the scapular region a short distance behind the

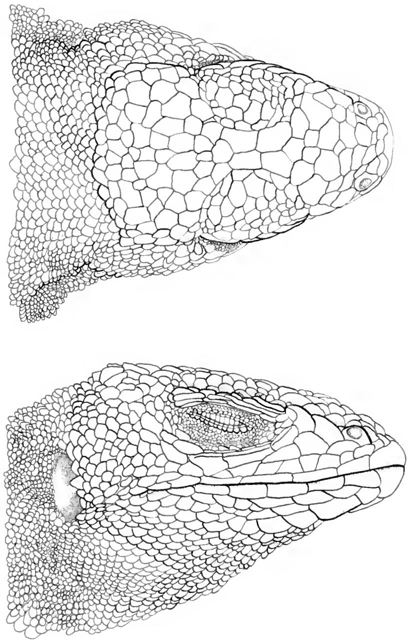

Fig. 26. *Stenocercus chlorostictus* (Holotype, male, SVL 66, ANSP 31760). Dorsal and lateral views of head. Perú: Depto. Cajamarca: Río Zaña, El Chorro, 1 km N (airline) Monte Seco, 1350m. Drawn by G. Bisbee.

forelimb. A fold confluent with the antehumeral fold extends dorsally to join the dorsolateral fold (the antehumeral fold thus has the appearance of a "Y," with one branch extending posterior over the scapular region, the other dorsally to the dorsolateral fold). Prominent gular fold continuous with antehumeral fold, widely separated midventrally from the corresponding gular fold on the opposite side. An antegular fold is continuous across the neck, delimited by a transverse series of very small scales between the ventral neck scales and scales of the throat. A moderately-developed oblique neck fold intersects the longitudinal neck fold and then continues a short distance ventrally and anteriorly. Postauricular folds well-developed; rictal folds weakly developed.

Tail. The tail is rounded. Dorsal caudal scales are large, very strongly keeled, mucronate and with moderately projecting spines. Caudal whorls alternate in size distally (most easily seen on the lateral surface of the tail). Ventral

caudal scales, except for a postanal series, are strongly keeled and mucronate.

Limbs. Dorsal scales of the fore- and hindlimbs keeled. Ventral scales of limbs smooth. Scales on the proximal ventral surface of forelimbs are very small, almost granular. Scales on posterior surface of thigh small, slightly protuberant, granular. Supradigitals smooth. Subdigitals multicarinate. Palmar scales keeled and somewhat mucronate; plantar scales smooth and mucronate.

Dermal pockets. No posthumeral pocket (Type 1); the skin surface is not modified, nor are there conspicuous folds (in LSUMNS 27231 there is a slight wrinkle in the skin of this area, but this is not consistent with the other specimens). Postfemoral pocket Type 3. The postfemoral pocket is a small bare patch of skin at the posterodorsal edge of the limb insertion followed by an overhanging fold of skin covered by granular scales. The postfemoral pocket of SDSU 1535 (male, SVL 75) is somewhat deeper than that of ANSP 31760 (male, SVL 66). In the female specimens, the postfemoral pocket is a bare patch of skin (LSUMNS 27231, 27233) or a slight depression covered by granular scales (LSUMNS 27232); in each case the patch is overhung by a slight fold of skin.

Pattern (Fig. 27). Males: Many dorsal head scales of the holotype and, less distinctly, SDSU 1535, have light centers with dark borders. In preservative the dorsum of males is dark gray or grayish brown with numerous blue-gray spots and a bold black light-bordered vertical bar in front of the forelimbs. The gular, pectoral, and posterior abdominal regions are suffused with dark gray (holotype) or are grayish white (SDSU 1535); otherwise the belly is grayish white. SDSU 1535 has vague gray reticulations surrounding large light areas ventrolaterally in the gular region. Females are brown with paired dorsal dark brown blotches, and heavily speckled with brown.

Scale counts and measurements (Table 1). This is a small-scaled species with moderately high scale counts. The tail is relatively short, averaging only about 1.4 times the body length (Tail/TL ratio 0.56-0.60).

Size.—The largest male is SDSU 1535 (SVL 75). The largest females (LSUMNS 27232-33) each have a SVL of 69.

Sexual dimorphism and Geographic Variation.— Because of the small available sample of this species, sorting out sexual and geographic variation is problematic. The available specimens do not suggest strong sexual differences in body size. The sexes differ strongly in pattern and coloration (see below). Standard meristic features of the holotype are encompassed within the range shown by the specimens from near Canchaque.

COLORATION.— *Coloration in Life*. The collector of the holotype stated that its "back was entirely green, including the tail. The belly was pinkish in the pectoral and abdominal regions, whitish in between." Color notes for the male paratype (SDSU 1535; R. Thomas, catalog in LSUMNS) are: "Dorsum green with pale green flecks; collar black. Throat orange to yellow on chest and buff on posterior venter. Underside of tail pinkish." Both male specimens show the light spotting on the dorsum in preservative (see below), so it is likely that these were light green in the holotype as in SDSU 1535, though not noted as such by the collector of the type.

Color notes for two of the females (LSUMNS 27231-32) from Canchaque are as follows: "Dorsum dark brown, markings darker, almost black. Venter and throats dull yellow (throats brighter); tongues yellow or yellow-pink." (R. Thomas, catalog entry for Field Numbers 3146-47).

Coloration in Preservative (Fig. 27). *Males*.— The type appears excessively darkened, perhaps due to strong formalin during fixation. The pattern of the two males is most evident with the specimens submerged in alcohol. The dorsal ground color of the neck, body, and tail is dark gray. The dorsal neck and body is covered with numerous blue-gray spots occupying 3-6 scales each (larger middorsally than more laterally). On the neck these spots tend to form irregular reticulations, but on the body they are arranged in irregular transverse rows. They fade gradually on the side of the

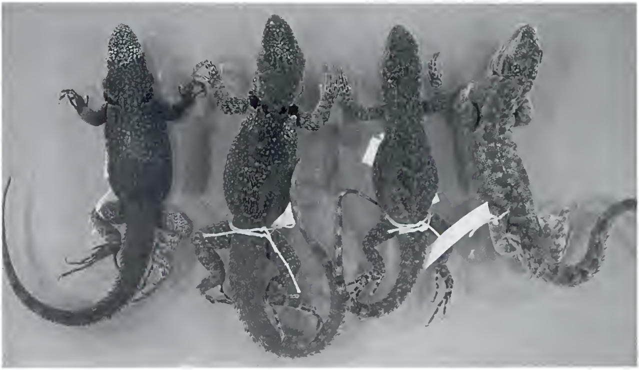

Fig. 27. Left to right: *Stenocercus chlorostictus* (Holotype, male, ANSP 31760, Depto. Cajamarca, Perú), *S. chlorostictus* (male, SDSU 1535, Depto. Piura, Perú), *S. chlorostictus* (female, LSUMNS 27232, Depto. Piura, Perú), *S. carrioni* (Holotype, male, BMNH 1946.8.11.83, Prov. Zamora-Chinchipe, Ecuador).

body. Just anterior to the forelimbs, a bold black vertical bar, bordered anteriorly and posteriorly by a narrow blue-gray line, extends from the anteroventral edge of the limb insertion dorsally onto the scapular region, forming a collar. In the male paratype, the bars of opposite sides approach one another closely middorsally, and each is marked by a constriction which makes it appear as though composed of two portions, one on top of the other; in the holotype, the bars comprising the collar are more widely separated middorsally (Fig. 27). In the holotype the posterior one third of the body is very dark, obscuring the dorsal spots (Fig. 27). Dorsal head scales are grayish white, each with a dark brown border. Lateral head scales dark gray. Dorsal surfaces of forelimbs dark gray with darker irregular markings. Dorsal surface of hind limbs blue-gray with dark brown markings, some of which form irregular bands. Most of the dorsal surface of the tail is dark gray, lightening toward the tip to reveal a pattern of alternating light and dark bands on the distal third. The ventral coloration of the two male specimens differs. In the holotype the ventral surface of gular region and anterior pectoral region heavily suffused with dark gray. The ventral scales for about 10 rows behind forelimb insertions are moderately suffused with dark gray; posterior to this, ventral scales of middle belly region are grayish white; posterior ventral scales (about 12 rows anterior to hindlimb insertions) are again heavily suffused with dark gray. Ventral scales of forelimb dark gray; of hind limbs, grayish white. Ventral scales of tail grayish white proximally, brownish gray distally. In the male paratype, the belly in general is lighter than in the holotype. The gular region is grayish white, with dark gray reticulations posterolaterally. The belly is grayish white, somewhat darker posteriorly; the ventral surface of the tail is whitish, becoming darker distally.

Females.— In the three females, the coloration in preservative is as follows: the dorsal ground color is brown to grayish brown (gray with loss of the stratum corneum) with dark brown irregular chevrons or paired paravertebral

spots (6 between the limbs). In LSUMNS 27231-32 there is a profusion of small dark brown spots and flecks dorsally and laterally. Dorsal surface of neck marked with irregular dark and lighter brown markings, sometimes forming reticulations. There is no suggestion of a prominent dark light-bordered antehumeral bar in the females. Dorsal surface of head brown to grayish brown with dark brown irregular markings. Dorsal surfaces of limbs brown with irregular dark brown markings that tend to form irregular bands. The tail is patterned as in the holotype except that the colors are brown to yellowish brown. Venter whitish with a profusion of dark brown speckling concentrated laterally. Gular region and ventral surface of neck whitish with heavy concentration of dark brown or gray pigment; superimposed on this is a series of large (3-4 scale diameter) regularly-spaced dark spots (prominent in LSUMNS 27231-32, more obscure in 27233). Ventral surface of limbs whitish with heavy concentration of brown or gray. Ventral surface of tail whitish proximally, gradually becoming suffused with dark pigment distally.

COMPARISONS.— *General Comparisons.* According to Fritts (1974), only three species of *Stenocercus* are primarily green dorsally: *S. haenschi* (Pacific versant of central Ecuador), *S. humeralis* (southern Ecuador), and *S. varius* (northwestern Ecuador). *Stenocercus chlorostictus* differs from all of these in having a very spiny tail and in color pattern (see Fritts, 1974). In addition, it differs from these species in the following characteristics (*S. chlorostictus* in parentheses): *S. haenschi* has fewer scales around the body, 57-62 (80-110) and lacks a postfemoral pocket (moderately developed); *S. humeralis* has more subdigital lamellae, 28-32, on the fourth finger (20-26), and has granular lateral body scales which grade gradually in size to the paradorsals (weakly imbricate, with a more or less abrupt transition to the paradorsals); *S. varius* has a strongly enlarged supraocular row and no antehumeral collar in males (absent and present, respectively), and a tail nearly twice the length of the body (Boulenger 1885:135).

In lacking a posthumeral pocket, *Stenocercus chlorostictus* differs from the following species of *Stenocercus*: *apurimacus*, *festae*, *nigromaculatus*, *ornatus*, *praeornatus*, *rhodomelas*, *roseiventris*, and *variabilis*. The following species of *Stenocercus* have deep postfemoral pockets, and thus differ from *Stenocercus chlorostictus*, which has a moderate postfemoral pocket (Type 3): *formosus*, *nigromaculatus*, *ochoai*, *praeornatus*, and *trachycephalus*.

Of the remaining species of *Stenocercus*, *S. chlorostictus* can be distinguished from the following by a greater number of scales around midbody (80-110; data for other species from Fritts [1974]): *chrysopygus* (54-82), *cupreus* (52-64), *ivitus* (44), *marmoratus* (43-54), *orientalis* (47-58), *melanopygus* (44-58), *moestus* (33-38), and *ornatissimus* (43-57). It differs from *crassicaudatus*, *festae*, and *nubicola* in having a very spinose tail and no vertebral crest, and from *empetrus* in coloration and extent of sexual dichromatism. *Stenocercus chlorostictus* differs from *S. eunetopsis* in having a proportionally shorter tail (Tail L/TL 0.56-0.60 versus 0.64-0.66), a less spiny tail, and in coloration. It differs from *S. boettgeri* in having smaller and less strongly keeled dorsal scales, a spiny tail, and in lacking a dorsal crest (very low crest in *S. boettgeri*).

Comparisons with Stenocercus simonsi Boulenger, 1899. Stenocercus chlorostictus is similar in overall form and many scutellational aspects to *S. simonsii*, though smaller and with a different pattern on the body in both sexes. The individual scales of *simonsii* are consistently smaller, sometimes much smaller, than corresponding scales in *chlorostictus*. This results in nearly all standard scale counts (except midbody scales) in *simonsii* being greater than those in *chlorostictus*. *Stenocercus simonsi* exhibits the following features which distinguish it from *chlorostictus* (characteristics in parentheses): (1) the number of scales comprising each supraorbital semicircle, counted from the canthus to the posterior corner of the orbit, is 13-14 (9-10); (2) the total number of supraorbital scales, counted as all scales between

the supraorbital semicircles and the superciliary row, is about 60 (about 40); (3) scales of the temporal region between the posterodorsal margin of the eye to the border of the ear, about 14 (9-11); (4) scales across the gular region 36-57 (34-42); (5) Paravertebral scales 90-120 (83-95); (6) lateral neck scales very finely granular (coarsely granular); (7) dorsal neck scales granular and not keeled (imbricate, keeled); (8) anterolateral scales of the trunk are finely granular (weakly imbricate and keeled); (9) caudal scales strongly mucronate and with acutely projecting spines (less mucronate and weaker spines). In addition, *S. simonsi* is not strongly sexually dichromatic, and males are not primarily green dorsally.

Comparisons with Stenocercus carrioni *Parker, 1934*. *Stenocercus chlorostictus* is essentially identical in scutellation to *S. carrioni*, which is known from southwestern Ecuador (the nearest localities for the two species are about 150km apart; Fig. 5). I discovered no discrete scale characters which unambiguously distinguish these species (see Table 1). However, the following characteristics will distinguish *chlorostictus* from *carrioni* (characteristics in parentheses; see Fig. 27): (1) strong sexual dimorphism in coloration and pattern (no sexual dimorphism in pattern detected). (2) light temporal stripe absent in males, and either absent or very vague in females (present in individuals of both sexes, but not consistently so, perhaps as a result of preservation artifact). (3) male coloration in life consisting of bright green dorsum with lighter green flecks, and a bold black collar in front of forelimbs; in preservative, dark gray with light flecks, and the bold collar still evident (preserved specimens only: paired dark paravertebral blotches on a brownish or greenish brown ground color; no dark collar in front of forelimbs). In addition, the antorbital scales in *chlorostictus* tend to have raised centers, giving a "cobblestone" appearance, whereas these scales lie flat in *carrioni*.

Stenocercus chlorostictus and *S. carrioni* are so similar that, before I had examined the male from the Canchaque population, I was unsure of whether to assign the three female specimens from this population to *carrioni* or to *chlorostictus*. There are strong similarities in coloration (in preservative) and pattern between females of these two species, and the lack of meristic differences between them makes assignment of females to either *carrioni* or *chlorostictus* difficult (it is, of course, possible, but I think doubtful, that the females from Canchaque will eventually be shown to be specimens of *carrioni*). Exacerbating this problem is the complete lack of information on geographic variation within either species. Until new samples of both *S. carrioni* and *S. chlorostictus* become available, so that color variation in life and geographic variation can be assessed, the species status of populations of either *carrioni* or *chlorostictus* for which only females are available will remain problematic. Presently, the heavily speckled dorsum and venter of females of *chlorostictus* and their lack of a distinct light temporal stripe appear to be the most reliable means of distinguishing them from females of *carrioni*.

NATURAL HISTORY OBSERVATIONS.—The type of *Stenocercus chlorostictus* was collected 5-6m above the ground in a tree in disturbed habitats along a road. Coffee plantations and brushy hillsides were nearby, and humid forest occupies the slopes above about 1500m at the type locality. That only a single specimen was obtained during extensive field work in the Río Zaña area (May-June 1987, January 1989) suggests that the species uses an infrequently-searched microhabitat (perhaps highly arboreal), or occurs only marginally in the area of intensive field work (1200m-2000m elevation). Two of the female paratypes (LSUMNS 27231-32) were collected in an adobe wall (R. Thomas, catalog entry for RT 3146-47).

Parker et al. (1985:170, under the name "Cruz Blanca") described the habitat in the general vicinity of the locality where the LSUMNS specimens of *Stenocercus chlorostictus* were collected. They noted that the west slope of the ridge east of Canchaque above 2150m is covered by a mixed evergreen forest, but much of the area below that eleva-

tion is disturbed or cleared land. Parker et al. (1985) reported that only scattered patches of forest remained below 2150m, where the LSUMNS and SDSU specimens of *Stenocercus chlorostictus* were collected (1740m) in 1974.

DISCUSSION

Pterygoid Teeth in *Stenocercus*

The use of pterygoid teeth as systematic characters in *Stenocercus* began with Boulenger's (1885 and following) notation of their condition in species descriptions. The presence or absence of pterygoid teeth assumed importance as characters for phylogenetic studies of *Stenocercus* and related genera with Etheridge's (1966) work, continued by that of Frost and Etheridge (1989) and Frost (1988). Because of their importance in phylogenetic analyses, it is important to clarify the intra- and interspecific distribution and variation of pterygoid teeth among species of *Stenocercus*, of which there are some contradictory observations.

All Stenocercini (*Stenocercus* sensu lato and *Proctotretus*) examined by Frost (1988:123) possessed pterygoid teeth (see Table 6 for species he examined). However, Boulenger (1885, 1899, 1900, 1901, 1911) observed their absence in some species of *Stenocercus*, and Griffin (1917), Parker (1934), and Noble (1924) reported them absent in *S. roseiventris*, *S. carrioni* and *S. nigromaculatus*, respectively. Etheridge (1966) reported pterygoid teeth "... Present or absent in *Liolaemus*, *Stenocercus*, and *Plica* . . . ." He did not state whether the variation was intra- or interspecific, and did not give details about the distribution of character states among species. Frost and Etheridge (1989) coded the state of pterygoid teeth "unknown" in *Polychrus* and *Leiocephalus* because of interspecific variability in these genera. However, they coded them as "present" in *Stenocercus*, despite prior observations that some species of *Stenocercus* lacked them. That there is possibly some variation (intraspecific and interspecific) in pterygoid teeth in *Stenocercus* is suggested by the fact that conflicting observations of pterygoid teeth are sometimes based on examination of different specimens of the same species. My observations on pterygoid teeth for the species discussed herein demonstrate both intra- and interspecific variability of this character. Hence, I summarize the known variation in this character in *Stenocercus*. However, no comprehensive study of variation in pterygoid teeth has been made for any species of *Stenocercus*.

Table 6 summarizes data for those species of *Stenocercus* in which pterygoid teeth have been reported as "absent." Included in footnote 1 to that table are all other species for which I have found reference to the pterygoid teeth, in these cases invariably as "pterygoid teeth present." In two cases I have confirmed other authors' observations by examining the same specimens they examined: the holotype of *carrioni* lacks pterygoid teeth, as reported by Parker (1934), and the specimen of *roseiventris* examined by Griffin (1917) also lacks them. Accepting previous observations at face value (Boulenger 1885, 1899, 1900, 1901, 1911; Griffin 1917; Frost 1988), nine species of *Stenocercus* (*boettgeri*, *crassicaudatus*, *humeralis*, *imitator*, *marmoratus*, *nigromaculatus*, *percultus*, *roseiventris*, and *varius*) show intraspecific variation for this character (personally confirmed by my observations on *boettgeri*, *imitator*, and *percultus*), whereas four others (*carrioni*, *eunetopsis*, *modestus*, *simonsi*) lack pterygoid teeth in all specimens examined (Table 6). Furthermore, *imitator* and *percultus* show intrapopulational variation in pterygoid teeth.

The components of variation in pterygoid teeth (intrapopulational, geographic, ontogenetic, sexual) have not been studied in any species of *Stenocercus*. The present observations on *percultus*, *imitator*, and *eunetopsis* do not suggest an obvious sexually dimorphic or ontogenetic component to the variation in these species (e.g., in *percultus*, for which only skeletons of males were available, the specimen lacking pterygoid teeth is also the largest; in *imitator*, one of two adult females lacked ptery-

Table 6. Variation in the presence of pterygoid teeth in species of *Stenocercus*. Only species for which pterygoid teeth have been reported as **absent** are listed in the table.[1] +, pterygoid teeth present; -, pterygoid teeth absent; N, not examined. Skulls of *eunetopsis*, *imitator*, and *percultus* examined during this study are listed in the osteological sections of the species accounts.

	Frost (1988)	Boulenger/Parker/ Griffin/Noble[2]	This study
boettgeri	+ (2)[3]	-	- (USNM 299613) + (MCZ 45843)
carrioni	N	- (holotype)[4]	- (MCZ 93589)[5]
crassicaudatus	+ (2)	- (as *torquatus*)	N
eunetopsis	N	N	- (2)
humeralis	+ (2)	-	N
imitator	N	N	+ (7)/ - (1)
marmoratus	+ (1)	-	N
moestus	N	-	N
nigromaculatus	+ (2)	- (MCZ 17975)	- (MCZ 18767)
percultus	N	N	+ (3) / - (1)
roseiventris	+ (1)	+ (Boulenger) - (Griffin)	- (CM 974, 4611)
simonsi	N	-	- (KU 134171) - (KU 134173)
varius	+ (1)	-	+ (USNM 201321)

[1] All other species for which the condition has been reported as "present" include the following (F, specimens examined by Frost 1988; W, specimens in MCZ examined by Ernest E. Williams and listed in the Appendix; C, specimens examined by me and listed in the species accounts or Appendix; B, reported by Boulenger in papers cited in footnote 2): *aculeatus* (W), *apurimacus* (F), *caducus* (F, W), *chrysopygus* (F, W, B), *cupreus* (F, W, B), *empetrus* (F), *erythrogaster* (F, W, C), *festae* (F), *formosus* (F, W), *guentheri* (F, W, C), *huancabambae* (C), *iridescens* (F, W, C), *melanopygus* (F, B), *ochoai* (F, W), *orientalis* (F), *ornatissimus* (F), *ornatus* (F), *praeornatus* (F), *rhodomelas* (F, C), *scapularis* (F), *trachycephalus* (W), *tricristatus* (F), *variabilis* (F, B).

[2] Data from Boulenger (1885, 1899, 1900, 1901, 1911), Parker (1934), Noble (1924), and Griffin (1917). All data are from Boulenger except those for *carrioni* (Parker), *nigromaculatus* (Noble), and *roseiventris* (Boulenger and Griffin). Griffin's (1917) assessment was apparently based on CM 974, which I confirmed in this study.

[3] Numbers in parentheses are the number of skulls examined by Frost (Appendix 1, Frost 1988) and during this study (see species accounts for *eunetopsis*, *percultus*, and *imitator*).

[4] Parker's observation of pterygoid teeth "absent" in *carrioni* was confirmed by my study of the holotype.

[5] MCZ 93589, KU 134171, KU 134173 are fluid-preserved specimens; all other citations of particular specimens in the table are derived from dry skeletons or cleared and stained preparations.

goid teeth; in *eunetopsis*, both specimens examined, male and female, lacked pterygoid teeth). The inconsistent observations among authors regarding pterygoid teeth in *Stenocercus* probably reflects greater variation in this character than has been recognized. Such variation is difficult to detect given the small sample sizes, usually only one or two per species, used in most osteological studies (though there are exceptions; cf. Etheridge 1966). The apparent variation in pterygoid teeth in *Stenocercus* suggests that additional work is needed before the phylogenetic significance of this feature can be interpreted with some security.

Similar variation also pertains to the related genus *Leiocephalus* (sensu Etheridge 1966). Etheridge (1966) reported pterygoid teeth present in *Leiocephalus carinatus*, *L. loxogrammus*, and *L. punctatus*, and absent in other species (16 species examined), whereas Frost (1988: 123) reported only *L. greenwayi* as lacking pterygoid teeth, and observed that other species, including seven species examined by Etheridge, possess them. Frost and Etheridge (1989) noted the interspecific variability in presence/absence of pterygoid teeth in *Leiocephalus*, but did not comment on the intraspecific variation apparent from their observations. I have not examined skeletal material of *Leiocephalus*. However, E. E. Williams examined skulls of *Leiocephalus* in MCZ for me (11 species, 16 subspecies, 32 skulls total) and confirmed the interspecific variability for this feature in *Leiocephalus*. Moreover, one skull of *L. carinatus* (12 skulls examined) lacked pterygoid teeth entirely (MCZ 141248) and another one possessed them on only one side (MCZ 141251), confirming intraspecific variability for pterygoid teeth in this species. One specimen of *L. stictogaster* (MCZ 59228) possessed one pterygoid tooth on one side only. The following species lacked pterygoid teeth for which Frost (1988) reported them as present: *inaguae* (MCZ 154263), *psammodromus mounax* (MCZ 54170, 86143), and *schreibersi schreibersi* (MCZ 59591-92). These observations suggest intraspecific variability for pterygoid teeth in *Leiocephalus*.

I conclude that there are as yet unexplored components of intra- and interspecific variation in pterygoid teeth in *Leiocephalus* and *Stenocercus*. The nature of this variation should be resolved more clearly so that its relevance to phylogenetic studies of this group of lizards can be evaluated more carefully. Studies designed to clarify the pattern of this variation should include a taxonomically broad array of species, and investigate sexual and ontogenetic change in pterygoid teeth.

Phylogenetic Relationships

No comprehensive phylogenetic treatment of *Stenocercus* (sensu lato) exists. Fritts (1974:18) presented a "Wagner dendrogram" showing relationships among species based on the quantitative method outlined by Kluge and Farris (1969). Since Fritts' (1974) analysis there have been considerable advances in understanding of methods of character analysis and coding (e.g., Maddison et al. 1984), and improvements in knowledge of character distributions and relationships among iguanians generally (e.g., Etheridge and de Queiroz 1988, Frost 1988, Williams 1988). I suspect that an analysis similar to Fritts' today might yield quite different results. Fritts (1974) chose not to erect subgeneric groups based on his analysis, and none has been formally proposed by other workers. However, Frost (1988:77), without extensive documentation, suggested that a large assemblage of species with reduced scale size (i.e., those species having small granular or subimbricate lateral body scales) formed a clade within *Stenocercus*. If the scale character proves to be phylogenetically informative upon more careful study, then *imitator*,. *eunetopsis*, and *chlorostictus*, described herein, would belong to this clade.

Given the present confusion surrounding the relationships among species of *Stenocercus* (sensu lato; see Introduction), and with the knowledge that several as yet undescribed species are presently known from northern Perú and southern Ecuador (E. E. Williams, pers. comm.; pers. obs.), it may be premature to

suggest hypotheses concerning relationships of the species described herein. Moreover, detailed descriptions for many species are nonexistent, and the only comprehensive treatment of the genus (Fritts 1974) does not adequately summarize variation in external characters for species of *Stenocercus*. Thorough study of osteological and other internal features has yet to be undertaken. Consequently, without taking on a complete revision of *Stenocercus*, identifying and interpreting characters that might be useful for detailed phylogenetic reconstructions at the species level is difficult.

I have not undertaken a comprehensive review of interspecific variation of external characters in *Stenocercus*. My examination of species assigned to *Ophryoessoides* by Fritts (1974) has been especially cursory. However, I have made detailed comparisons of the species described herein with a broad array of other species of *Stenocercus*, particularly phenotypically similar ones. My conclusions concerning the relationships of species described herein should be viewed as tentative, and subject to revision once character distributions are more comprehensively surveyed. Hence, some of the rather strong similarities between the species here described and other species of *Stenocercus*, although noteworthy, may or may not contain relevant cladistic information. Other features are interpretable as shared derived characters based on broader surveys among tropidurine iguanians (Frost 1988). In this discussion I focus on both the phenetic resemblances and possible synapomorphies, which perhaps indicate supraspecific groupings for species of *Stenocercus* discussed herein. Nevertheless, even those characters considered synapomorphies herein still must be reexamined in the context of a broader sampling of both characters and taxa than I have attempted. Some such characters are possible synapomorphies for a more inclusive set of species than considered here.

From the outset of this study it was apparent that three species described here (*percultus*, *eunetopsis*, and *chlorostictus*) showed detailed resemblance to other species of *Stenocercus* from the Pacific versant of southern Ecuador. The exception to this pattern among Pacific versant species, the strong resemblance between *S. imitator* and *S. praeornatus*, is considered further below. In general, species of *Stenocercus* from the Amazonian versant, and species generally distributed north and south, respectively, of 2° S latitude and 8° S latitude, were quite dissimilar to the western Andean species described here. In the cases of *Stenocercus imitator*, *S. eunetopsis* and *S. chlorostictus*, the similarities to other species (*praeornatus*, *simonsi*, and *carrioni*, respectively) are so close as to require especially careful delineation of the defining characteristics of the new species relative to those previously described (see Comparisons in the Species Accounts). The interpretation of these similarities as synapomorphies is problematic, however. Nonetheless, in each case except one (*imitator*/*praeornatus*), certain characters shared between these species pairs are interpretable as derived, and such shared *combinations* of characters may suggest close phylogenetic relationship between members of each pair. In other words, closely related species are expected to possess a common series of derived features, even though some characteristics may appear singly in other species of *Stenocercus*. I now consider these cases in greater detail.

The strong similarities between *Stenocercus imitator* and *S. praeornatus* have been extensively documented in the species account for *imitator*. This is the only case in which an Amazonian species, or one south of 8° S latitude, shows a strong resemblance to a species here described from the western versant of the Andes. Note that Fritts' assertion that *Stenocercus praeornatus* (in his sense including the western Andean populations I assign to *S. imitator*) and *S. boettgeri* shared similar distribution patterns was based on his erroneous inference about the type locality of *boettgeri* (see discussion in the species account for *S. imitator*). Despite the strong similarities in scutellation and color patterns between *imitator* and *praeornatus*, I have been unable to identify any of the features they share as un-

equivocally derived. The color pattern of females of both species is similar to that of some other species in the genus (see, e.g., comparisons with females of *S. percultus* above). Individual elements of the male coloration in the two species (e.g., black gular collar, rose/lavender belly coloration) appear elsewhere in the genus as well. Nevertheless, the similarities in scutellation and male coloration in *imitator* and *praeornatus* are too detailed to dismiss easily without greater understanding of the evolution of these characters in *Stenocercus*. In other words, does the strong phenetic resemblance between *imitator* and *praeornatus* indicate close relationship? More comprehensive study of external and internal features among species of *Stenocercus* will be necessary to resolve this question.

Stenocercus eunetopsis and *S. simonsi* share several features which are unusual in *Stenocercus*: (1) caudal scales extremely spinose; (2) variably-developed shallow mite pockets present under the antehumeral fold (shared also with some specimens of *carrioni*, *cupreus*, and *chrysopygus*); and (3) strong similarity in overall color pattern (an unusual one in *Stenocercus*), despite slight differences in coloration and intensity of dorsal pattern (see species account); males lack ventral flash colors. Comparable spinose tails are found elsewhere in the genus only in *S. marmoratus* and *S. roseiventris* (both of which have more strongly spinose tails than either *simonsi* or *eunetopsis*). Frost (1988:207) indicated that a tail armed with strongly mucronate and spinose scales was a derived characteristic within the Stenocercini. The antehumeral mite pockets are weakly-developed and unlike the deep pockets present among neck folds in *Tropidurus* (Rodrigues 1987), but antehumeral mite pockets are unusual in iguanians generally (Frost 1992). Although there are differences in modal scale counts, sizes, and extent of keeling, the scale differences between *simonsi* and *eunetopsis* are rather minor in comparison to the strong similarities in overall form, coloration, and extent of sexual dimorphism. In combination with the characteristics of tail armament and mite pockets within the antehumeral folds, the similarities in coloration and scalation are taken as indicative of close relationship between *S. simonsi* and *S. eunetopsis*. It is perhaps worth noting also (though emphasizing the caveat that only few specimens have been examined) that pterygoid teeth are absent in all samples of *simonsi* and *eunetopsis* examined.

Stenocercus chlorostictus and *S. carrioni* are so similar in form and scalation that, were it not for the strong sexual dimorphism and distinctive male coloration in the former, the two species would be practically indistinguishable. Without more extensive analysis of geographic variation (which will require more samples than now exist), females of these two species are possibly not reliably distinguishable. The strongly spinose caudal scales (though similar in these two species to some other species, e.g., *S. crassicaudatus*), as well as the relatively short tails, are derived features within *Stenocercus*, although not unique to *chlorostictus* and *carrioni*. However, given their close geographic proximity (Fig. 5) along with detailed similarities in squamation, body form, neck fold development, and mite pocket form, I hypothesize a close relationship between *carrioni* and *chlorostictus*.

Further evaluation of the relationships of *eunetopsis*, *simonsi*, *carrioni*, and *chlorostictus* is not attempted here. However, the geographic proximity and similarities between *S. eunetopsis* and *S. empetrus* discussed earlier (Species Accounts) warrant further exploration of the possible relationship of *empetrus* to (*eunetopsis* + *simonsi*) as knowledge of the genus improves. In addition, evaluation of the relationships of (*chlorostictus* + *carrioni*) should consider some other somewhat unusual features of these species: the presence of antehumeral mite pockets and absence of pterygoid teeth (again, with only small samples examined) in *carrioni* (shared with *simonsi* and *eunetopsis*), and the green coloration of *chlorostictus* (shared with *haenschi*, *humeralis*, *varius*; see Fritts 1974). Unfortunately, the distribution of these charac-

ters among species of *Stenocercus* is not well known. The problematic interpretation of pterygoid teeth in *Stenocercus* has already been noted. I discovered four species of *Stenocercus* which have antehumeral mite pockets in at least some individuals (see species account for *simonsi*), but there has been no comprehensive study of this character in *Stenocercus*. The green coloration of male *chlorostictus* is unusual in *Stenocercus*, and its possible significance relative to the relationships between *chlorostictus* and other "green" species should be investigated more thoroughly. In general, however, *chlorostictus* appears to be quite different in most characters from *humeralis* and *varius*, which are larger lizards with much longer tails (Note: Gunther's [1859] description of *humeralis* stated that the tail was not quite one and one-half times as long as the head + body, and Boulenger [1885] stated that in *humeralis* the tail was only slightly longer than the body, and that the gular scales were granular; however, none of the USNM series of *humeralis* that I examined had granular gular scales, and in individuals in which the tail was complete, it measured about twice the SVL; clearly, their identity should be verified with reference to other specimens). Additionally, green coloration may not be as rare in *Stenocercus* as Fritts (1974) thought: I have seen individuals of both *S. crassicaudatus* and *S. boettgeri* that were basically green in life, and some male specimens of *imitator* have green dorsal pigment, especially on the head (see species accounts). Color descriptions of additional *Stenocercus* species would aid in evaluating the phylogenetic significance of coloration in the genus. The knowledge that a small subset of species have a primarily green dorsal coloration is presently only a potential clue to a broader supraspecific grouping. In the context of these possible indicators of broader groupings, it is worth noting that *simonsi*, *carrioni*, and *empetrus* (along with *crassicaudatus*) appeared as a derived clade within one branch of Fritts' (1974:18) phylogenetic hypothesis.

Finally, the two species of "large-scaled" *Stenocercus* described here (i.e., those species having a covering of large imbricate scales on the body), *percultus* and *huancabambae*, are similar to one another, and to several other "large-scaled" species of Ecuador and Perú. Specimens of each were misidentified in museum collections as *ornatus*, *iridescens*, and *scapularis* (*S. percultus*), or *aculeatus* and *iridescens* (*S. huancabambae*). Of these, *scapularis*, *iridescens*, and *aculeatus* are generally considered members of the genus *Ophryoessoides* (sensu Fritts 1974), and *huancabambae* also fits the external criteria for this genus (see species account; *percultus* lacks the distinctly enlarged posterior head scales and keeled ventral scales characteristic of *Ophryoessoides* sensu Fritts 1974). Several undescribed "larged-scaled" species of *Stenocercus* (*Ophryoessoides* sensu Fritts 1974) are presently known from Perú and Ecuador (E. E. Williams, pers. comm.), and consideration of character distributions among all of the included species will be necessary before the similarities can be interpreted phylogenetically with some confidence. Nevertheless, I suspect *percultus* to be closely related to some of the other "large-scaled" species of *Stenocercus* from western Ecuador and northern Perú; *huancabambae* shares derived characteristics with at least one described species of *Stenocercus* from northern (Amazonian) Perú and Ecuador, as documented below.

In the case of *percultus* there are strong similarities in overall form (vertebral crest development, posthumeral and postfemoral pocket development, neck fold development, tail form), and in some aspects of coloration and pattern, to two species of western Ecuador, *ornatus* and *rhodomelas* (see species accounts for detailed comparisons). Of the shared characteristics of these species, the deep posthumeral and postfemoral pockets (Types 4 and 5, respectively) are clearly derived (these pockets are absent in *Leiocephalus*, and plesiomorphically absent within *Stenocercus* fide Frost [1988:181]). In fact, *percultus*, *ornatus*, and *rhodomelas* are the only described species of *Stenocercus* sensu Fritts (1974) which have *both* pockets so extensively developed (pocket

type inferred from brief characterizations given in Fritts [1974] for species not examined in this study; some species of *Ophryoessoides* sensu Fritts [1974] have comparably-developed posthumeral and postfemoral pockets). The other shared features of *percultus*, *ornatus*, and *rhodomelas* are more difficult to interpret. Some, such as the well-developed projecting vertebral crest, are probably plesiomorphic within *Stenocercus*, and coloration features are not easily polarized with present knowledge. Nevertheless, the unusual combination of deep posthumeral and postfemoral mite pockets are here interpreted as derived characters suggestive of a possible close relationship among these three species; other shared features, once properly interpreted, may provide additional corroborative evidence.

Stenocercus huancambambae is phenotypically similar to an array of *Stenocercus* species (as here conceived) having enlarged head scales, large imbricate body scales, keeled ventrals, and relatively long tails (genus *Ophryoessoides* sensu Fritts 1974). It is unclear that these species form a clade within the expanded *Stenocercus*, however, and Frost (1988) suggested that *Ophryoessoides* sensu Fritts (1974) was possibly polyphyletic. *Stenocercus huancabambae* does possess two features that appear to be uncommon in *Stenocercus*, and therefore here considered derived features: a single canthal scale on each side, and enlarged, angulate temporal scales bearing a projecting blade. Both of these characters are shared with *S. aculeatus*, a species distributed parapatrically or narrowly allopatrically east of the distribution of *huancabambae* in northern Perú and eastern Ecuador. Both features may appear singly or in combination in other species of *Ophryoessoides* (sensu Fritts 1974), several of which are undescribed (E. E. Williams, pers. comm.). Single canthals occur in some other species of *Stenocercus* (e.g., some *empetrus*), but all species that possess angulate temporals *with a projecting blade* would be assigned to *Ophryoessoides* using Fritts' (1974) external criteria for that genus (recall that other species, such as *percultus*, have strongly keeled angulate temporals without a projecting blade). *Stenocercus huancabambae* and *S. aculeatus* are the only two species of which I am aware that possess *both* features. Hence, the close geographic proximity of *huancabambae* and *aculeatus*, and their joint possession of two unusual scale characters, possibly indicates a close relationship between these species. Indeed, Williams (1988) advocated the use of geographic information in interpreting character evolution and synapomorphy; the canthal and angulate temporal pattern shared by *huancabambae* and *aculeatus* may be so interpreted using Williams' (1988) Rule of Geographic Continuity. However, until these features are more comprehensively studied in *Stenocercus* (especially among species of *Ophryoessoides* sensu Fritts 1974), I can do little more than offer them as potential synapomorphies shared by *aculeatus* and *huancabambae* which warrant further investigation. (All species of *Leiocephalus* and most species of the *Tropidurus* group of iguanians [Etheridge and de Queiroz 1988] examined possessed two or more canthals; some *Plica* examined possessed single canthals. No *Leiocephalus* or *Tropidurus*-group of iguanians of which I am aware possess projecting angulate temporals).

In summary, the relationships hypothesized for the species of *Stenocercus* described herein are of three patterns: (1) three species of the Pacific versant (*eunetopsis*, *chlorostictus*, *percultus*) are suggested to have their relationships with species of *Stenocercus* of southwestern Ecuador (respectively, with *simonsi*, *carrioni*, and one or more large-scaled species including *ornatus* and *rhodomelas*); (2) *imitator*, also of the Pacific versant, is possibly related to *praeornatus* of the Amazonian versant of central Perú, although none of the strong resemblances between these species are unambiguous synapomorphies; and (3) the close relationship of *huancabambae* to the geographically contiguous *aculeatus* is supported by two synapomorphies of head scalation, both of which appear singly in some other species of *Stenocercus*. The implications of these hypoth-

esized relationships will be discussed with respect to general distribution patterns of *Stenocercus* in northern Perú and Ecuador in the following section.

Distribution Patterns and Biogeography

Figs. 28-29

Stenocercus in the broad sense used here is primarily distributed in the Andes (Colombia to Bolivia) and adjacent lowland areas (western Ecuador and Perú, and the upper Amazonian region of Ecuador, Perú, and Bolivia). A few species (*caducus*, *tricristatus*, and several undescribed species; genus *Ophryoessoides* sensu Fritts 1974) are distributed in eastern South America away from the Andes and its immediately adjacent lowlands. My purposes in this section are (1) to summarize local patterns of elevational and ecological distribution of species in the vicinity of Monte Seco (Bosque Monteseco, Río Zaña valley, Pacific versant, Depto. Cajamarca, Perú), which has been the focus of much of my field experience with this genus; (2) to consider patterns of elevational stratification in other areas of northern Perú and compare these to the pattern in the Río Zaña valley; (3) to examine the association of a set of co-occurring species of *Stenocercus* with relict humid forests on the west slope of the Andes in northern Perú, and to assess the relevance of these co-occurrences to the history of those forests and to forests further north in western Ecuador; and (4) to comment on other prominent distributional patterns of *Stenocercus* in the Huancabamba Deflection region of Ecuador and Perú.

Local Distribution and Sympatry of Stenocercus in the Monte Seco Region, Rio Zaña Valley, Depto. Cajamarca, Perú (Fig. 28).— In the Río Zaña valley four species of *Stenocercus* are known from about 1000m-2600m elevation. *Stenocercus imitator* has a broad elevational range in this region (1200m-2600m), whereas *percultus* (800m-1600m), *eunetopsis* (2450m-2600m), and *chlorostictus* (1300m) are much more restricted elevationally. *Stenocercus percultus* and *S. imitator* occur sympatrically from about 1200m-1600m, and both are sympatric with *S. chlorostictus* at the only elevation at which it is known to occur in this region. At higher elevations (>2400m) *imitator* occurs sympatrically with *eunetopsis* in presently non-forested habitats in the Río Udima valley [according to Koepcke (1961) this region was once covered with "mesothermic and oligothermic rainforest"].

Stenocercus imitator is not only the most broadly distributed species elevationally. It was also the most abundant species and occurred in more general types of habitats (primary and secondary forest, agricultural land, chapparal-like thickets, grassland) than the other species. The microhabitat distribution of *imitator* was equally broad, unlike the other species: it was observed on the ground, vertical rock faces, on logs and fence rows, and up in trees. Despite the breadth of environments used by *S. imitator*, where it occurred in microsympatry with other species of *Stenocercus*, there may be slight differences among the species in their behavior and microhabitat use (see species accounts). The most striking example of this, the sympatry between *imitator* and *eunetopsis*, is illustrated by observations that a microhabitat commonly used by *eunetopsis* (crevices in the ground) was underutilized by *imitator* in the same area (see species account for *eunetopsis*). The rarity of *chlorostictus* in the Río Zaña collection suggests its preference for a microhabitat, perhaps highly arboreal, not used by the other sympatric species.

Elevational Stratification and Sympatry an other areas of northern Perú (See Fig. 29 For Physical Features And Localities Mentioned In This Section).—The local distribution of *Stenocercus* in the Río Zaña valley illustrates a general pattern common to other areas in Perú, namely, segregation of species along elevational and microhabitat gradients within local regions. In the Department of Piura, for example, the Cordillera Huancabamba rises to about 3100m and separates Pacific drainages from the Río Huancabamba, which eventually drains south-

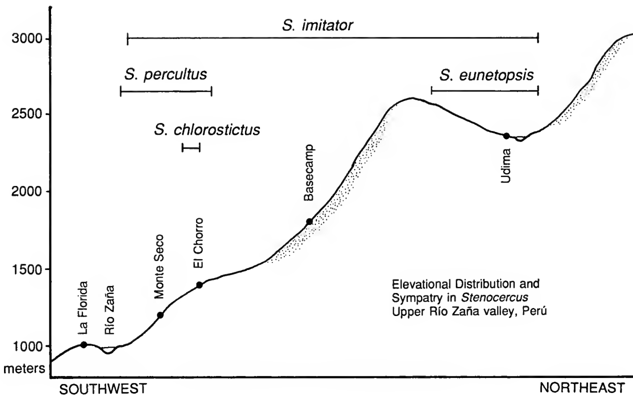

Fig. 28. Schematic diagram of elevational and horizontal distributions of species of *Stenocercus* in the vicinity of Monte Seco, Depto. Cajamarca, Perú. The transect generally follows a line drawn between La Florida and Udima (see Fig. 6). Approximate elevations are given on the left. The lower elevational extent of *imitator* and *percultus* to the west and southwest is not presently known. Shading indicates the approximate extent of humid forest remaining on the slopes (1989), although many areas within the forest are subject to local disturbance.

eastward into the Río Marañon. A transect from the Pacific lowlands, across the Cordillera Huancabamba, and into the valleys of the Río Huancabamba and Río Marañon reveals eight species of *Stenocercus* presently known. Of these, six are recorded from the western slopes and summit of the Cordillera Huancabamba. *Stenocercus iridescens*, although not known from the lowlands adjacent to the Cordillera Huancabamba, occurs in dry habitats below 1000m in northern Perú south to at least the vicinity of the Abra de Porculla (Fig. 4), and very likely is generally distributed in the arid lowlands in Perú north of this area. Three other species of *Stenocercus* (*chlorostictus*, *imitator*, and *percultus*) are known from about 1700m-1850m on the Pacific versant of the Cordillera Huancabamba (vicinity of Canchaque), whereas two other species, *ivitus* and *nubicola*, are known from the summit at 3100m (Fritts 1974). Immediately east of the continental divide in the Río Huancabamba valley *S. nigromaculatus* is known from about 1900-2300m (Fritts 1974). Still further to the east *S. huancabambae* is known from below 1000m closer to the main course of the Río Marañon, where it is broadly sympatric with another tropidurid, *Tropidurus stolzmanni* (Dixon and Wright 1975). Additional collecting in this area will undoubtedly close the gaps between the elevational ranges of these species, assuming that suitable habitats still remain, for this area is subject to great human disturbance (Parker et al. 1985). The sympatry of three species of *Stenocercus*, as noted here for the Monte Seco region and the vicinity of Canchaque, is the greatest number of sympatric species documented within this genus, although collections from the Río Tarma valley (Amazonian versant, Depto. Junín, Perú; unpublished observations) suggest the possi-

Fig. 29. Major physical features and place names for the area of northern Perú and southern Ecuador under discussion. Shaded area is the Andes; stippled area is above 1000m; hatched area is above 3000m.

bility of four sympatric species of *Stenocercus* there.

Parapatry among closely related species is a common distribution pattern of amphibians and reptiles of the Peruvian Andean slopes (Cadle and Patton 1988), although, with the exception of patterns within *Stenocercus* documented here, all other examples are from the Amazonian slopes. However, similar patterns of parapatry on the western slopes occur in other taxa (e.g., small mammals; Pearson and Ralph 1978, Pearson 1982), and are to be expected for amphibians and reptiles, even though diversity of amphibians and reptiles along Pacific versant

gradients is relatively low. Such distributions along elevational gradients suggest models to evaluate alternative mechanisms for geographic differentiation (Cadle and Patton 1988), once more data concerning relationships among the species are available.

Distribution of Stenocercus in Relict Forests of the Cordillera Occidental of Northern Perú.— The existence of humid forests along the western slope of the Andes in northern Perú has been widely known since botanical and ornithological explorations earlier this century (Chapman 1926, Weberbauer 1936). Becoming increasingly mesic, such forests also exist with ever greater restriction and isolation along the western Andean front to almost 16° S (M. Koepcke 1958, H. Koepcke 1961, Simpson 1975b). M. Koepcke (1958) and H. Koepcke (1961) postulated that these forests once formed a more or less continuous band of vegetation compressed between the lowland arid formations and the nonforested montane habitats (jalca) above tree line. Paleoclimatic models for the region (Simpson 1975a, 1975b) hypothesize greater humidity in the Andes during the Pleistocene, which may have resulted in greater extension of montane humid forests along the western Andes. Presently, deforestation and the relatively arid climate of the west coast of South America combine to make these forests increasingly relictual.

Very few elements of the fauna or flora of the montane humid forests of the western Andes have been studied in detail, but several studies have noted that many taxa share a distribution comprising populations (or a series of closely related species) in relictual forests of the western Andes in northern Perú and southern Ecuador (H. Koepcke 1961, M. Koepcke 1961, Koepcke and Koepcke 1958, Simpson 1975b). In fact, M. Koepcke (1961) reported several species of birds with distributions parallel to that reported here for several *Stenocercus* species (viz., with populations in the upper Río Zaña, and near the Abra de Porculla and Canchaque). Other species in these Pacific slope forests are known to occur east of the continental divide in the low intermontane basins in northern Perú (e.g., M. Koepcke 1961, Lamas 1982, for bird and butterfly distributions, respectively), where rainshadow effects create a complex mixture of arid and more humid forests (Barbour and Noble 1920; Chapman 1926; Weberbauer 1936, 1945; Parker et al. 1985). The generally low elevation of the Cordillera Occidental in this region would facilitate such west to east exchange, given sufficient extent of mesic habitats induced by past climatic changes (Simpson 1975b).

With respect to the fauna and flora of Bosque Monteseco, the distributions of several species of *Stenocercus* and other amphibians and reptiles provide further evidence that elements of this community are characteristic of several relict forest patches on the Pacific versant or interandean valleys of the Cordillera Occidental of northern Perú (M. O. Dillon, pers. comm.; Dillon and Cadle 1991), and that some of these species are closely related to others in western Ecuador. This discussion focuses on the species of *Stenocercus*, and notes other amphibians and reptiles sharing similar distribution patterns.

Three species of *Stenocercus* from the western Andes of northern Perú (*chlorostictus*, *percultus*, *imitator*) co-occur at two localities that are presently the southern and northern limits, respectively, known for each species: the vicinity of Monte Seco (Depto. Cajamarca) and the vicinity of Canchaque (Depto. Piura). Furthermore, I predict that at intermediate localities where one or more of these species occurs, the others also eventually will be found (assuming original habitats remain). For example, at the Abra de Porculla (Depto. Piura) *percultus* and *imitator* are known to co-occur, and I predict that *chlorostictus* may eventually be found there. *Stenocercus percultus* is also known from the upper Río Reque between the Abra de Porculla and the Monte Seco region (Fig. 4), and I suspect that *chlorostictus* and *imitator* will be found there as well. These three species of *Stenocercus* are indicative of a distinctive fauna that is largely endemic to the relict forests of the western Andes of northern

Perú (see additional faunal and floral examples in Koepcke 1961). Each site from which these species are recorded is known to have isolated patches of mesic to humid forest similar in form, if not species composition, to that at Bosque Monteseco (H. W. Koepcke 1961), but these forests are not now continuously distributed in this region. They are subject to greater restriction due to substantial human pressure in this area presently.

Furthermore, the phylogenetic relationships here postulated for the species of *Stenocercus* inhabiting the humid forests of the western Andes of northern Perú collectively suggest historical connections with similar montane communities of southwestern Ecuador. If the species pairs *chlorostictus/ carrioni* and *eunetopsis/simonsi* are correctly identified, then the biogeographic links between the Peruvian and Ecuadorian montane forests of the western Andes is clear. Although a similar precise relationship is not here postulated for *Stenocercus percultus*, it appears to be closely related to a cluster of species occurring in southwestern Ecuador (see Phylogenetic Relationships) and, hence, provides further biogeographic evidence for a historical relationship among forested communities of the western Andes. The pattern is strengthened by observations that, with respect to *Stenocercus*, the faunas of the Pacific and Amazonian versants of the Andes are quite distinct (further discussed below), although overlap in the Amazonian and Pacific faunas with respect to other taxa occurs in the Huancabamba Deflection region.

Similar distributional patterns are evident with respect to other elements of the Bosque Monteseco herpetofauna. These include the following species with populations or closely related species in western Ecuador or in the low intermontane basins of the Huancabamba Deflection: (1) *Dendrophidion brunneum* (Colubridae), for which the Río Zaña valley is the only reported Peruvian locality, but which is known from several localities on the western versant of the Andes in Ecuador (Lieb 1988); (2) *Stenorrhina degenhardti* (Colubridae), now known from northern Perú as well as western Ecuador (Peters and Orejas-Miranda 1970; unpublished observations); (3) *Coniophanes longinquus* (Colubridae), known only from the Monte Seco region, but closely related to *C. dromiciformis* of southwestern Ecuador (Cadle 1989); and (4) *Macropholidus ruthveni* (Teiidae) and *Eleutherodactylus lymani* (Leptodactylidae), known from the interandean valleys of the Huancabamba Deflection of northern Perú and/or southern Ecuador (Noble 1921, Lynch 1969). As is the case for the species of *Stenocercus* from Bosque Monteseco, the Río Zaña valley is presently the southernmost known locality for each of these species, but they may eventually be found in other relict forests along the Andean slopes to the south, and perhaps further north as well.

The Amazonian and Pacific Slope Faunas of Stenocercus.— In the context of the large number of examples of distribution patterns showing clear associations between the faunas of the Río Zaña valley, and those of western Ecuador or the intermontane valleys of the Huancabamba Deflection, the detailed similarity (? indicating relationship) between *Stenocercus imitator* and *S. praeornatus* of the Amazonian versant of central Perú must be viewed as unusual. Further study will be required to determine whether the suggested relationship between *imitator* and *praeornatus* can be corroborated, and whether other species of the Río Zaña valley flora or fauna show a similar pattern. Nevertheless, the potential relationship between *imitator* and *praeornatus* prompts a more careful consideration of distribution patterns of *Stenocercus* on both sides of the Andes.

Presently, only a few species of *Stenocercus* are documented from both Pacific and Atlantic drainages. Most of these, including *S. guentheri*, *S. festae*, *S. humeralis*, and *S. ornatus*, are distributed in the low intermontane basins in the vicinity of Loja and surrounding areas in southern Ecuador. In this region the Andes reach 3000m or greater in only a few disjunct areas (Figs. 4, 5, and 29), and most of these species occupy the broad highland valleys there be-

tween about 2000m-2500m. North of about 1° S latitude a continuous chain of peaks >3000m elevation exists, and only *S. guentheri* is reported on both Amazonian and Pacific versants north of this region.

A topographic situation similar to that in southern Ecuador exists in northern Perú, with continuous highland > 3000m beginning about 7° S latitude (Fig. 29). In Perú, however, only *Stenocercus chrysopygus* is documented below 3000m on both Amazonian and Pacific versants. It is known from both sides of the Cordillera Blanca in the Río Marañon (Amazonian) and Río Santa (Pacific) drainages up to 3500m (Departments Huánuco and Ancash), but is not recorded from the high Andes at these latitudes (4500m-5000m; Fritts 1974). Two other species, *S. ivitus* and *S. empetrus*, are known from the continental divide or highland areas above 3000m that span both Pacific and Amazonian drainages, but their distributions are not known to extend into intermediate elevations (< 3000 m) on either versant. Even in the relatively low region of the Huancabamba Deflection, the distinction between the Amazonian and Pacific species of *Stenocercus* is absolute. Those species known from the Pacific versant near the Abra de Porculla, for example, are not recorded east of the continental divide. Thus, there is little suggestion of free interchange between Amazonian and Pacific faunas as far as present distribution patterns of *Stenocercus* are concerned. This may reflect the fragmented nature of suitable habitats now present in this area, although some species of plants and birds (Simpson 1975b) have disjunct distributions on either side of the Andes south of the Huancabamba Deflection. Simpson (1975b) showed that virtually all species showing such distributions on both sides of the Andes south of 8° S occurred at least as far north as the Huancabamba Deflection region, and she postulated previously more continuous distributions for them through the low-lying Huancabamba Deflection area. If *Stenocercus imitator* is the sister species of *S. praeornatus*, then this species pair is possibly representative of this pattern (now as disjunct vicariant species).

In the context of evaluating possible connections between the Pacific and Amazonian versant faunas, two specimens of *Stenocercus* from the Pacific versant of the Andes in northern Peru (LSUMNS 26990, 35238; Cajamarca and Ancash departments, respectively) are potentially of great interest. Although their taxonomic status has not been a focus of this study, my attention was called to them because they are similar enough to *Stenocercus orientalis* (known only from the Cordillera Oriental of Amazonas department, Perú) to warrant close comparison with that species. Their possible relationship to *orientalis* should be re-evaluated as more material becomes available. Although present samples do not allow their unequivocal assignment to species, the two Pacific versant specimens differ from *orientalis* (characteristics in parentheses) by the following: They have a somewhat enlarged supraocular row (supraoculars subequal); head scales, other than a few posterior ones, are smooth or wrinkled, but not distinctly keeled (distinctly keeled); scales of the parietal-occipital region are larger than in *orientalis*; the scales of the temporal region are weakly keeled (strongly keeled); postfemoral pocket type is 3 (4-5).

The Huancabamba Deflection Region as a Faunal Barrier for Stenocercus, and other Distributional Patterns in the Genus.— The Huancabamba Deflection region is widely recognized as a major biogeographic discontinuity for Andean organisms (e.g., Vuilleumier 1969, Simpson 1975b, Duellman 1979, Parker et al. 1985). The low altitude of the Andes in this region causes fragmentation of montane habitats, and introduces a complex mixture of environments. Distribution patterns of *Stenocercus* in northern Perú and southern Ecuador also reflect the influence of this discontinuity, in that no species of *Stenocercus* is presently known from north, as well as south, of the Huancabamba Deflection region, despite considerable diversity within or adjacent to this area. Of the five species described herein, and eight others known from the Andes of Perú north of 8° S latitude (*melanopygus*, *empetrus*,

orientalis, *chrysopygus*, *nubicola*, *ivitus*, *ornatissimus*, *nigromaculatus*) none is recorded from Ecuador. On the other hand, eight or more montane species of *Stenocercus* (*humeralis*, *simonsii*, *ornatus*, *festae*, *rhodomelas*, *carrioni*, and at least two undescribed species) are known from southern Ecuador (south of 3° S latitude) but are not recorded from northern Perú. Hence, although particular species pairs may be represented both north and south of the Huancabamba Deflection (e.g., *Stenocercus eunetopsis/simonsi*) the faunas are quite distinct at the species level. In this respect, the distribution patterns of species of *Stenocercus* are similar to those in many other groups of organisms, which often extend up to, but do not cross, the Huancabamba Deflection region (Duellman 1979).

Although the distinction between the species of *Stenocercus* known north and south of the Huancabamba Deflection is great, in fact many of the montane species of *Stenocercus* appear to have distributions that are restricted in latitudinal or elevational extent, or both (this observation must be tempered with the realization that knowledge of the fauna in many areas where they occur is very poor). Particularly in regions of complex topography and physiography, as in northern Perú and southern Ecuador, species' distributions often appear to be very localized. Many, for example, are known from single drainage systems (e.g., *simonsi*, *eunetopsis*, *orientalis*, *nigromaculatus*). This suggests that exploration of many of the more poorly known river systems in northern Perú and southern Ecuador will result in discovery of new species of *Stenocercus*, much as the discovery of four new species resulted from my field work in the Río Zaña valley. Hence, the diversity within the genus may be much greater than presently recognized.

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APPENDIX—SPECIMENS EXAMINED

The detail in which the following specimens were examined varied. Extensive scale counts were made on some; others were examined only for particular features such as the mite pockets or head scale patterns. [S] indicates a dry skeletal preparation examined for osteological characters. As noted in the Introduction, species of *Ophryoessoides* are here referred to *Stenocercus*. In addition to these specimens, reference was made to specimens of *Leiocephalus* and to members of the *Tropidurus* group (sensu Etheridge and de Queiroz 1988, Frost 1988, Frost and Etheridge 1989) housed in ANSP.

Stenocercus sp.: *COLOMBIA*: DEPTO. SANTANDER: San Gil (ANSP 24136). ***Stenocercus*** sp. (cf. ***haenschi***): *ECUADOR*: ? DEPTO. AZUAY: Km 94, Guayaquil to Cuenca (CAS 94788). ***Stenocercus*** sp.: *PERÚ* DEPTO. ANCASH: 31 km (by road) E Pariacoto, 9000 ft. [2750m] (LSUMNS 35238). DEPTO. CAJAMARCA: Km 134 on road from Pacasmayo to Cajamarca (LSUMNS 26990). ***Stenocercus aculeatus***: *ECUADOR*: PROV. PASTAZA: 2.5km downstream from Caveceras, Río Bobonaza, 2150ft. [655m] (USNM 200885). Cabeceras del Río Bobonaza (USNM 200886-88). Vera Cruz (ca. 10km E Puyo), 3300ft. [1030m] (USNM 200889-90). Near Puyo (USNM 200891). Montalvo, Río Bobonaza (USNM 200892). Alto Río Oglan (USNM 200893). Río Villano (USNM 200894). Río Pucuyacu, Río bobonaza (USNM 200895). Río Licuna, tributary of Río Villano (USNM 200896). Palanda, E of Sarayacu (USNM 200897). Immediate environs of Arajuna, 537m (USNM 200898). Río Liguino (USNM 200899). Río Pastaza, Alpayaca (MCZ 8061 [S]). ***Stenocercus boettgeri***: *PERÚ*: DEPTO. JUNÍN: 28km SW (by road) San Ramón, 2070m (USNM 299613 [S]); 16km NNE Palca, 2540m (USNM 299545-48); Huacapistana, 2500m (FMNH 40617);

Huachon (MCZ 45843 [S]); DEPTO. PASCO: Huancabamba (FMNH 3945-46). ***Stenocercus caducus***: *BOLIVIA*: PROV. SANTA CRUZ: Buenavista (MCZ 24883 [S], 29022 [S]). ***Stenocercus carRíoni***: *ECUADOR*: PROV. EL ORO: Cordillera de Chilla, Llano de Guavos (AMNH 18308); Río Lunam (AMNH 22185). PROV. LOJA: Alamor (MCZ 34866, 133220; AMNH 21847, 22136-37, 22140, 22154, 22157, 22170, 22177, 22193-94, 22197, 22201-02, 22207-08); 10km N Celica, 1900m (MCZ 93589). PROV. ZAMORA-CHINCHIPE: Zamora, 3250ft. [990m] (BMNH 1946.8.11.83 [Holotype; formerly 1933.6.24.75]). ***Stenocercus chrysopygus***: *PERÚ*: DEPTO. ANCASH: Anexo Llupa, Provincia y Distrito Huaraz (ANSP 31840-42). Yungay, 2335m (FMNH 81426-34, 81503-08). Recuay (FMNH 3944). Tecapam [=Ticapampa] (FMNH 3943); Huar z region (MCZ 45832 [S]). ***Stenocercus crassicaudatus***: *PERU*: DEPTO. CUZCO: San Fernando, Río Cosireni (MCZ 12401-02). ***Stenocercus cupreus***: *PERÚ*: DEPTO. HUANUCO: Ambo (FMNH 5606-14). Pachachupan, slightly above Acomayo on Hu nuco-Tingo Maria Rd., about 2300m (USNM 193681); Hu nuco (MCZ 43789 [S], 43790-92; FMNH 16169, 16178-79). ***Stenocercus empetrus***: *PERÚ*: DEPTO. LA LIBERTAD: Otuzco (FMNH 5708); Huamachuco, 3350m (KU 134380-84, 134391). DEPTO. CAJAMARCA: Cajamarca, 2800m (FMNH 3941-42, 5710-11; KU 134411-13; BMNH 1900.3.30.1-3); Baños (MCZ 8084); 15km SW Encanada, 3110m (MCZ 172059); Celend2n (MVZ 78777-78); 3km E Celend2n (KU 134414-20). ***Stenocercus erythrogaster***: *COLOMBIA*: (ANSP 8607 [Type]). ***Stenocercus festae***: *ECUADOR*: PROV. AZUAY: S edge of city of Cuenca near Río Tomebamba, 8365ft [2550m] (USNM 201209-10); 1 km SE Cuenca, 8365ft [2550m] (USNM 201211-13); 18km N Cuenca, 2400m (CAS-SU 25544); 8km N Cuenca (CAS-SU 25626, CAS 93921-24, 93929-30). ***Stenocercus formosus***: *PERÚ*: DEPTO. JUNIN: 17km (by road) SW San Ramón, 1510m (USNM 299615); Chanchamayo (MCZ 11295 [S]). ***Stenocercus guentheri***: ECUADOR: locality uncertain, Prov. Pichincha or Prov. Chimborazo (ANSP 18162-168, 18242, 32719). PROV. PICHINCHA: Quito (USNM 222584 [S]); Río Islaya? (FMNH 27674); Machachi (MCZ 8418 [S], 8423 [S]. PROV. TUNGURAHUA: Oriente, Ambato (FMNH 36711-12). ***Stenocercus humeralis***: *ECUADOR*: DEPTO. LOJA: 1km W Loja, 6800ft [2070m] (USNM 201264-69). Loja (MCZ 89875). El Empalme, Valle de Casanga (USNM 201257-63); Km 25 on Pan American Highway between Loja and Cuenca (CAS 94111-12). ***Stenocercus iridescens***: *ECUADOR*: "western Ecuador" (ANSP 8583). Not located: Canas (MCZ 8066). PROV. CHIMBORAZO: Huigra (USNM 61755). PROV. EL ORO: Buena Vista, 100ft. [30m] (USNM 200956); Machala (FMNH 197964); 7km SSE Machala (USNM 222585 [S]); Pasaje, 100ft. [30m] (USNM 200946-54); Santa Rosa (USNM 200977-80). PROV. ESMERALDAS: about 5 km E Esmeraldas (MCZ 84163). PROV. GUAYAS: Guayaquil (MCZ 84156, 84158, 84166, 8412 [S], 84161-62 [S], 84165 [S], 84168 [S], 84171-72 [S]; USNM 12175, 12281, 200981); Milagro, Hcda. San Miguel, 200ft [60m] (USNM 200982); Estero de Soledad, near Río Chirate, 5m (USNM 222797-99). PROV. IMBABURA: 1km SW Penaherrera on trail down to Río Intac, 1950-2000m (USNM 200912 [S], 200913); Penaherrera, 1825m (USNM 200914-17). PROV. LOJA: Río Cazanga valley, 1000m (MCZ 85089-90). PROV. LOS RÍOS: Vinces, Hcda. El Triunfo (USNM 222800); Jauneche, near Pampa Ibarra (USNM 222801); Quevedo (USNM 200921-34). PROV. MANABI: 12km NNE Jipijapai (USNM 200935); 4km W Calceta (USNM 200936-38); San Clemente, between Charapoto and Bahia, sea level (USNM 200940); San Vicente, across bay from Bahia de Caraquez, sea level (USNM 200941-45). PROV. PICHINCHA: Hacienda Cerro Chico, 46 km N Quevedo (MCZ 151711). Centro Cientifico Río Palenque, 47 km S Santo Domingo de los Colorados on road to Quevedo (MCZ 154583, 156137, 156849). *PERU*: no locality (FMNH 81450). DEPTO. LAMBAYEQUE: 21km E and 7km N Olmos, 2300ft. [700m] (MVZ 82364; locality is on the road between Olmos and the Abra de Porculla [R. B. Huey, field notes, MVZ]). DEPTO. PIURA: near Huasimal on Cascadero trail near Ecuador border, Amotape Mountains (FMNH 9835, 9837). ? DEPTO. TUMBES: Quebrada Cimmaron, Amotape Foothills (FMNH 9805). ***Stenocercus marmoratus***: *BOLIVIA*: DEPTO. COCHABAMBA: Totora, 2600m (USNM 94093). ***Stenocercus melanopygus***: *PERÚ*: DEPTO. CAJAMARCA: Baños, 2800m (MCZ 126133 [syntype]). ***Stenocercus nigromaculatus***: *PERÚ*: DEPTO. PIURA: Huancabamba (MCZ 17975 [type], 18767 [S]). ***Stenocercus ochoai***: *PERÚ*: DEPTO. CUZCO: Hcda. Urco, near Calca, 9500ft. [2510m] (FMNH 34123-26, 34134-36, 34138); Ollantaytambo (MCZ 41984 [S]). ***Stenocercus ornatissimus***: *PERÚ*: DEPTO. LA LIBERTAD: Carabamba, Prx. Cajabamba (MCZ 154240). DEPTO. LIMA: Distrito San Pedro de Casta, Prov. Huarochiri, Marcahuasi (ANSP 31837-38). ***Stenocercus ornatus***: *ECUADOR*: PROV. LOJA: 1-1.5 Km E Loja, 6800 ft.

[2070m] (USNM 201270-71, 201273-74); 3 km E Loja, 6900 ft. [2100m] (USNM 201276-79). ***Stenocercus praeornatus***: *PERÚ*: DEPTO. JUNIN: Comas, 3220m (KU 134224-28, 134232). ***Stenocercus rhodomelas***: *ECUADOR*: PROV. AZUAY: 7-8km W Girón, 2100m (USNM 201280, 201289). Approximately 3-4km E San Francisco, Km 109 on Cuenca-Machala Highway, 1250m (USNM 201293, 201298; 222586-588 [S]). Santa Isabel (USNM 201305-06, 201310, 201315). ***Stenocercus roseiventris***: *BOLIVIA*: DEPTO. SANTA CRUZ: Prov. del Sara, 350m (MCZ 126140; CM P973-74). Buenavista, Prov. del Sara, 500m (CM S4560, S4589, S4610-11). Santa Cruz de la Sierra (CM S4628). *BRASIL*: EST. ACRE: Alto Purús (MCZ 133219). *PERÚ*: DEPTO. PUNO: Sandia, Tambopata, San Juan, 1520m (FMNH 64755, 64757). ***Stenocercus simonsii***: *ECUADOR*: PROV. AZUAY: Oña, 2000m (BMNH 1946.8.11.73-74 [syntypes]); Girón, 2240-2500m (KU 134157-64). PROV. LOJA: Saraguro, 2500m (KU 134165-74). ***Stenocercus trachycephalus***: *COLOMBIA*: DEPTO. CUNDINAMARCA: Aguadita, S of Bogotá (ANSP 24161); Bogotá (ANSP 26253). ***Stenocercus varius***: *ECUADOR*: PROV. PICHINCHA: Llambo (USNM 201318-20, 201321 [S], 201322).

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Systematic Revision of the Asian Catfish Family Pangasiidae, with Biological Observations and Descriptions of three New Species

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ABSTRACT.—The Pangasiidae comprises two genera, *Pangasius* Valenciennes, 1840 and *Helicophagus* Bleeker, 1858. *Pangasianodon* Chevey, 1930, *Pteropangasius* Fowler, 1937, and *Sinopangasius* Chang and Wu, 1965 are synonyms of *Pangasius*. Study of type specimens and other material of Pangasiidae (39 nominal species or subspecies) results in recognition of 18 previously described species as valid. *Helicophagus hypophthalmus* Sauvage, 1878 is a valid species of *Pangasius* and senior synonym of *P. sutchi* Fowler, 1937, which should henceforth be known as *P. hypophthalmus* (Sauvage, 1878). *Pteropangasius cultratus* (Smith, 1931) and *Sinopangasius semicultratus* Chang and Wu, 1965 are synonyms of *Pangasius pleurotaenia* Sauvage, 1878 and *Pangasius krempfi* Fang and Chaux, 1949, respectively. *Pangasius paucidens* Fang and Chaux, 1949, *P. ponderosus* Herre and Myers, 1937, and *P. tubbi* Inger and Chin, 1959, are synonyms respectively of *P. gigas* (Chevey, 1930), *P. nasutus* Bleeker, 1862, and *P. micronema* Bleeker, 1847. *Pangasius bocourti* Sauvage, 1878 and *P. djambal* Bleeker, 1846 are valid species. Three new species are described, *P. myanmar* from Myanmar, *P. conchophilus* from the Chao Phraya and Mekong basins, and *P. kinabatanganensis* from northeastern Borneo, bringing to 21 the total number of species recognized in Pangasiidae. The generic type species, *P. pangasius*, is restricted to India, Pakistan, and Bangladesh, where it is the only pangasid, and Myanmar. Thailand has 11 species, Indonesia ten, and peninsular Malaysia only three. Four species are apparently endemic to the island of Borneo. Some species have extremely rapid growth, particularly *P. gigas*, which attains 300 kg or more and apparently can grow to at least 200 kg in its first three years. Apparent adaptations for rapid growth include voracious or gluttonous feeding behavior; specialized larval dentition; and abdomen, alimentary canal, and vent capable of exceptional expansion. Although most species are confined to fresh water, *P. polyuranodon* frequently occurs in brackish tidal reaches, and at least two species, *P. pangasius* and *P. krempfi*, occur in the sea. The latter species, previously known only from the South China Sea, is reported from the Mekong River for the first time.

The molluscivorous genus *Helicophagus* comprises two species, *H. wandersii* Bleeker, 1858 from Sumatra and the Chao Phraya and Mekong basins, and *H. typus* Bleeker, 1858, from Sumatra and perhaps Borneo. They have marked differences in shape of oral and palatal toothbands and in numbers of gill rakers and anal fin rays. [distribution, food habits, *Helicophagus*, larvae, *Pangasius*, reproduction]

Considerable confusion has attended identification of species of the tropical Asian catfish genus *Pangasius*. Most nominal species, based on type specimens from Thailand, Indo-China or Indonesia, were proposed by workers without access to comparative material from outside their respective regions. Smith (1931) and Fowler (1935; 1937) each described several species from Thailand, which has more pangasiids than any other country, without consulting the other's type specimens or those of species described from other countries. Nearly all authors have had problems recognizing juveniles of the larger species, and Smith, Fowler, and others created junior synonyms based on small specimens. There has been no previous attempt at a systematic revision of the genus. Particular confusion has surrounded the species *P. pangasius*. Our studies indicate that it is confined to South Asia, i.e. Pakistan, Bangladesh, India, and Burma, and that reports from Thailand, Laos, Vietnam, Kampuchea, Malaysia, and Indonesia are based on misidentifications of several species.

The nominal species of Pangasiidae and their identification resulting from our studies are listed in Table 1. All are referred to *Pangasius* with the exception of *P. hexanema* Bleeker, 1852, and *P. longibarbis* Fowler, 1934, both now identified as *Laides hexanema* (Bleeker). Perhaps the most noteworthy systematic change is the recognition of *Helicophagus hypophthalmus* Sauvage, 1878, as a valid species of *Pangasius* and senior synonym of the important aquaculture species *P. sutchi* Fowler, 1937.

Observations and comments on biology are given in the systematic accounts of each species. Among the more interesting are those on specialized larval teeth in *P. gigas* and *P. larnaudii*; rapid growth rate in *P. gigas*; gluttony in *P. conchophilus* and several other species; occurence of *P. pangasius* and *P. krempfi* in the sea; and sexual dimorphism and scratches in *P. macronema*.

The most important pangasiid species currently utilized in aquaculture are *P. pangasius* (India), *P. hypophthalmus* (Thailand), and *P. djambal* (Indonesia, particularly Java). Additional species that may have potential use in aquaculture include the large and fast growing species *P. gigas*, *P. larnaudii*, and *P. sanitwongsei*, and, in ponds with molluscs, *P. conchophilus*.

In the material examined for each species, care has been taken not only to give the locality, but also, when available, date of collection. There are two reasons for including the date. In many instances, due to environmental deterioration, species no longer occur in the same areas. Thus it has been many years since *P. pleurotaenia* and *P. larnaudii* were last collected in the Meklong basin, and perhaps they no longer occur there. On the other hand, some species have been widely spread in recent years by transportation of wild caught or hatchery reared stock, and their distribution prior to introduction should be documented. It is our intention that the information in this revision eventually will be incorporated into computerized data bases on biodiversity of Thailand and Southeast Asia, and for this purpose dates of occurrence are essential.

Although *Pangasius gigas* certainly was on the verge of extinction, due to the artificial breeding and introduction program carried out by the Department of Fisheries and National Inland Fisheries Institute of Thailand since 1984 the species no longer is endangered. At present none of the species of *Pangasius* seems endangered or threatened, but serious decline of some species has occurred in some river basins, e.g. the giant species *P. sanitwongsei* is no longer common in the Chao Phraya basin and the status of its population there is unknown.

Numerous fossils from Tertiary deposits in central Sumatra have been identified as a species of *Pangasius*, *P. indicus* (Marck 1876), by Sanders (1934). The material is deposited mainly in the Geological Museum, Bandung. Some of the specimens are in the ZMA (pers. comm. Han Nijssen, 1985). This is the only fossil record of the family Pangasiidae to come to our attention. We have not studied the material, and do not refer to it or to *P. indicus* again in this paper.

The mollusk-eating genus *Helicophagus*

Table 1. Nominal species and subspecies of Recent Pangasiidae and their present identification if different.

Nominal species	Present identification
Pangasius aequilabialis Fowler, 1937	*Pangasius macronema*
Pangasius altifrons Durand, 1940	*Pangasius bocourti*
Pangasius beani Smith, 1931	*Pangasius sanitwongsei*
Pangasius bocourti Sauvage, 1880	
Pangasius burgini Fowler, 1937	*Pangasius larnaudii*
Pangasius conchophilus new species this paper	
Pteropangasius cultratus (Smith, 1931)	*Pangasius pleurotaenia*
Pangasius delicatissimus Bleeker, 1862	? *Pangasius macronema*
Pangasius dezwaani Weber & deBeaufort, 1912	? *Pangasius micronema*
Pangasius djambal Bleeker, 1846	
Pangasius fowleri Smith, 1931	*Pangasius pleurotaenia*
Pangasianodon gigas Chevey, 1930	*Pangasius gigas*
Pangasius hexanema Bleeker, 1852	*Laides hexanema* (Schilbeidae)
Pangasius hoeksi Hardenberg, 1948	? *Pangasius micronema*
Pangasius humeralis Roberts, 1989	
Helicophagus hypophthalmus Sauvage, *1878*	*Pangasius hypophthalmus*
Pangasius juaro Bleeker, 1852	*Pangasius polyuranodon*
Pangasius kinabatanganensis new species this paper	
Pangasius krempfi Fang & Chaux, 1949	
Pangasius larnaudii Bocourt, 1866	
Pangasius lithostoma Roberts, 1989	
Pangasius longibarbis Fowler, 1934	*Laides hexanema* (Schilbeidae)
Pangasius macronema Bleeker, 1851	
Pangasius micronema Bleeker, 1847	
Pangasius myanmar new species this paper	
Pangasius nasutus Bleeker, 1862	
Pangasius nasutus. Smith, 1945 (misident.)	*Pangasius conchophilus*
Pangasius nieuwenhuisii (Popta, 1904)	
Pangasius nieuwenhuisi. Inger & Chin, 1962 (misident.)	*Pangasius kinabatanganensis*
Pangasius pangasius (Hamilton, 1822)	
Pangasius pangasius godavarii David, 1962	*Pangasius pangasius*
Pangasius pangasius upiensis Srivastava, 1968	*Pangasius pangasius*
Pangasius paucidens Fang & Chaux, 1949	*Pangasius gigas*
Pangasius pleurotaenia Sauvage, 1878	
Pangasius polyuranodon Bleeker, 1852	
Pangasius ponderosus Herre & Myers, 1937	*Pangasius nasutus*
Pangasius rios Bleeker, 1851	*Pangasius micronema*
Pangasius sanitwongsei Smith, 1931	
Sinopangasius semicultratus Chang & Wu, 1965	*Pangasius krempfi*
Pangasius sutchi Fowler, 1937	*Pangasius hypophthalmus*
Pangasius taeniura Fowler, 1935	*Pangasius larnaudii*
Pseudolais tetranema Vaillant, 1902	*Pangasius micronema*
Pangasius tubbi Inger & Chin, 1962	*Pangasius micronema*
Helicophagus typus Bleeker, 1858	
Helicophagus waandersii Bleeker, 1858	

comprises two species, *H. typus* Bleeker, 1858 and *H. wandersii* Bleeker, 1858, with remarkably different dentition and gill rakers. The survival status of *H. typus* is uncertain. It has been reported only from Palembang, Sumatra, and Bandjermasin, Borneo; identification of the Borneo material needs confirmation, and the most recent specimens from Palembang were collected in 1908. *Helicophagus waandersii*, otherwise known only from Palembang, is common in lowland portions of the Mekong and Chao Phraya basins.

MATERIALS AND METHODS

This revision is based on a large amount of material deposited in systematic reference collections in North America, Europe and Thailand, including nearly all of the extant type specimens of all nominal species of Pangasiidae. We have designated a neotype for *P. djambal* Bleeker, 1846. The material is deposited in the following institutions: Academy of Natural Sciences of Philadelphia, ANSP; British Museum (Natural History), BMNH; California Academy of Sciences, including specimens formerly deposited in the Natural History Museum, Stanford University, CAS and CAS-SU; Field Museum of Natural History, Chicago, FMNH; Institute for Breeding Research, Tokyo University of Agriculture, IBRP; Kasetsart University Museum of Zoology, Bangkok, KUMF; Musée Guimet d'Histoire Naturelle, Lyon, MGHNL; Muséum National d'Histoire Naturelle, Paris, MNHN; National Inland Fisheries Institute, Bangkok, NIFI; Naturhistoriska Riksmuseet, Stockholm, NRM; Riksmuseum van Naturlijke Historie, Leiden, RMNH; Royal Ontario Museum, Toronto, ROM; University of Michigan Museum of Zoology, Ann Arbor, UMMZ; National Museum of Natural History, Smithsonian Institution, Washington, D.C., USNM; and Zoological Museum of Amsterdam, ZMA.

In the list of material examined, type material is cited first; non-type material is listed by river basins from N to S and then W to E, or vice versa. Specimens with locality data consisting only of a country or geographical area are listed last.

Counts and measurements follow the definitions of Hubbs and Lagler (1947), with minor exceptions. Thus "head" is measured from tip of snout to upper angle of gill opening. Counts of vertebrae in catfishes including Pangasiidae are problematical, especially when obtained from radiographs, due to difficulty in enumerating the largely fused anterior vertebrae of the "Weberian complex." In general, we have considered the first free centrum as representing the fifth vertebra. In Pangasiidae this centrum often but not always bears the first pair of ribs (invariably large and readily visible in radiographs). Since completion of the manuscript, we have been informed that in catfishes the sixth vertebra is the anteriormost rib-bearing vertebrae (pers. comm. Carl Ferraris). If this holds in Pangasiidae, then the majority of the abdominal and total vertebral counts reported in this paper should be increased by one.

In reporting locality data we generally report the original locality data as indicated by original labels or catalog entries, occasionally correcting obvious spelling errors or omissions. When substantive additions to the original locality information are made, they are enclosed in brackets. If modern equivalents are given, they are placed in brackets, but in general modern equivalents are not given unless there is reasonable certainty that they are indeed equivalent. Some localities for material examined have no modern equivalent, e.g. "Laos Siamois" and "Cambodge" for specimens reported on by Sauvage. Many of the specimens were obtained from markets, although the source is not always known. In collections made by the first author specimens obtained from markets are always so indicated, thus "Ubol Ratchatani market." The older the specimens, the more likely that they were caught near the market, but in recent years fresh fish from central Thailand (Chao Phraya basin) has been transported to markets in Ubol Ratchatani and other localities in the Mekong basin and probably also to markets in the Meklong basin.

The main objective of this paper has been to

provide a complete systematic revision of the species of Pangasiidae. Some comments are made about relationships among species, such as the evidently close relationship between *P. hypophthalmus* and *P. gigas*, but we have not made a detailed study of relationships within the family. Our generic classification is conservative, and virtually no changes in generic classification originate in this paper. Thus, the decision to place *Pangasianodon gigas* in *Pangasius* (rather than placing *Pangasius hypophthalmus* in *Pangasianodon*) is a conservative or pragmatic one. Likewise we retain *P. pleurotaenia* in *Pangasius* rather than in the monotypic *Pteropangasius*. Others may feel that some of the species herein placed in *Pangasius* should be assigned to different genera, but we believe that adequate information to define such genera is lacking, and that their recognition at this time would be too subjective and not contribute to nomenclatural stability.

SYSTEMATIC ACCOUNTS

PANGASIIDAE

Pangasiidae are large catfishes (full grown adults 20 cm to about 3 m, most species attaining 50 cm or more), with maxillary barbels, a single pair of mental or mandibular barbels, and no nasal barbels; posterior nostril about same size as anterior nostril and lying behind or slightly medial to it. Branchiostegal rays 7-11. Adipose fin invariably present. Pelvic fin with 6 or 8-9 rays. Anal fin rays 26-46. Principal caudal fin rays 8/9. Vertebrae 39-52. Two genera, *Pangasius* and *Helicophagus*.

Pangasius, with 19 species, occurs in the Indian subcontinent, Burma, Indo-China, Malaysia, and Indo-China. The species exhibit a wide range of feeding behaviors. *Helicophagus*, with two species, feeds on molluscs and occurs in Thailand, Indo-China, and Indonesia. It differs from *Pangasius* in having a much narrower mouth and snout, much more elongate ethmoid portion of skull, and palatal dentition consisting of two vomerine tooth patches (palatine tooth patches absent).

Pangasius, *Helicophagus*, and their presumed relatives have been placed by various authors either in Pangasiidae (Weber and de Beaufort 1913; Roberts 1989) or in Schilbeidae (Smith 1945; Inger and Chin 1962). No adequate definition has been given of these families, and various authors have not been in agreement on the genera to be placed in them. *Laides* Jordan, 1919, although hitherto placed in Pangasiidae by Roberts (1989) and several other authors, is closely related to Asian genera placed by all authors in Schilbeidae, such as *Clupisoma* Swainson, 1838, and *Eutropiichthys* Bleeker, 1862. Previously known only from the generic type species, *Laides hexanema* (Bleeker 1852) from Thailand, Indo-China, and Indonesia, *Laides* is a senior objective synonym of *Proeutropiichthys* Hora, 1937, and perhaps also of *Clupisoma*, with numerous nominal species in the Indian subcontinent and Burma. *Platytropius sinensis* Hwang, 1987, described from the Mekong in Yunnan, is very closely related to *L. hexanema*, differing from it mainly in having nasal barbels, slightly more numerous anal fin rays, and more vertebrae. We have identified this species, which should be known as *Laides sinensis* (Hwang), in the Mekong basin in Thailand, and in collections from Pahang, Malaysia. *Laides*, *Clupisoma*, and *Eutropiicthys* agree with each other and differ strikingly from *Pangasius* and *Helicophagus* in having a well developed nasal barbel (absent only in *L. hexanema*); two pairs of mandibular barbels lying in deep longitudinal grooves in isthmus; posterior nostril much larger than anterior nostril, on top of snout and relatively close to middle of head (i.e., strongly medial to anterior nostril), and its opening transversely oriented. *Silonia* Swainson, 1838, with two species in the Indian subcontinent and Burma, bears a superficial resemblance to *Pangasius* but differs in having highly specialized enlarged canine teeth and posterior nostril enlarged, medial to anterior nostril, and transversely oriented. Thus, although it agrees with Pangasiidae in having only a single pair of mandibular barbels and no nasal barbels, the condition of the nostril places it with the Asian genera of Schilbeidae. Whether

these Asian genera belong in the same family with *Schilbe* Oken, 1817, and other endemic African genera of Schilbeidae is a question beyond the scope of this revision. Preliminary observations by the second author indicate that in pangasiids the main axis of the olfactory lamellae is longitudinal, whereas in Schilbeidae it is transverse. This difference is particularly noticeable when comparing genera such as *Laides* and *Pangasius*.

Pangasius Valenciennes

Pangasius Valenciennes *in* Cuvier and Valenciennes, 1840:45 (type species *Pimelodus pangasius* Hamilton, 1822, by monotypy and absolute tautonymy).

Pseudopangasius Bleeker, 1862a:399 (type species *Pangasius polyuranodon* Bleeker, 1852, by original designation and monotypy).

Pseudolais Vaillant, 1902:51 (type species *Pseudolais tetranema* Vaillant, 1902 = *Pangasius micronema* Bleeker, 1847, by monotypy). See Weber and de Beaufort, 1913:261.

Neopangasius Popta, 1904:180 (type species *Neopangasius nieuwenhuisii* Popta, 1904, by monotypy).

Pangasianodon Chevey, 1930 (type species *Pangasianodon gigas* Chevey, 1930, by monotypy).

Pteropangasius Fowler, 1937:142 (type species *Pangasius cultratus* Smith, 1931 = *Pangasius pleurotaenia* Sauvage, 1878, by original designation and monotypy).

Sinopangasius Chang and Wu, 1965:11 (type species *Sinopangasius semicultratus* Chang and Wu, 1965 = *Pangasius krempfi* Fang and Chaux, 1949, by monotypy).

Pseudopangasius was defined as having palatal dentition consisting of a median vomerine tooth band and two palatine tooth bands. As such it would include *P. polyuranodon*, *P. nasutus*, *P. conchophilus*, *P. myanmar*, *P. bocourti*, and *P. djambal*. This group evidently represents a polyphyletic assemblage, and we would not recognize *Pseudopangasius* even as a subgenus.

Pseudolais is based on a single juvenile specimen subsequently identified as *P. micronema* (Weber and de Beaufort 1913:261).

Neopangasius was defined by Popta (1904:180) as having palatal teeth in a single large patch. This serves to identify a possibly monophyletic group of four species known only from Borneo: *P. humeralis*, *P. kinabatanganensis*, *P. lithostoma*, and *P. nieuwenhuisii*. The species tend to have somewhat high vertebral counts (Table 3), and *P. humeralis* and *P. nieuwenhuisii* also agree in having a greatly enlarged pectoral gland associated with a very elongate humeral process, a trait not shared with any other species. *Neopangasius* may be recognized as a subgenus of *Pangasius*.

Pangasianodon, based on two large individuals, 2 and 2.5 m, was defined by Chevey (1930) as having no teeth or mandibular barbels; at such large size gill rakers also are absent. Smaller individuals up to 500 mm, however, do have oral teeth, mandibular barbels, and gill rakers, thus agreeing in these as in other respects with species placed in *Pangasius*. As pointed out by Durand (1949), *P. gigas* and *P. hypophthalmus* agree with each other and differ from all other species of *Pangasius* in usually having 8 (occasionally 9) instead of only 6 pelvic fin rays. *Pangasius gigas* and *P. hypophthalmus* further agree with each other, and differ from all the other species in having a terminal mouth, with teeth of upper jaw entirely covered by lower jaw when mouth is closed. As first pointed out by Durand, young of *P. gigas* and *P. hypophthalmus* are so similar that it is difficult to distinguish them; he concluded, largely on the basis of the 8-9 pelvic fin rays, that *Pangasianodon* should be retained as a valid genus including two species, *P. gigas* and *P. hypophthalmus*. While we agree that the two species are each other's closest relative and form a monophyletic unit, we prefer to treat *Pangasianodon* as a subgenus of *Pangasius*.

Pteropangasius differs from all other *Pangasius* in having the abdomen keeled for its entire length, from the vent to between the pectoral fin base, rather than keeled only between vent and base of pelvic fins. Its large eye, head shape, low gill raker count, thin-walled, black-pigmented intestines, and plant-eating

habits indicate a possible close relationship to species in *Pangasius* such as *P. micronema* and *P. polyuranodon*. Its distinctive color pattern, with distinct midlateral and abdominal stripes separated at the level of the pectoral fin base, is also found in several species of *Pangasius*.

Pteropangasius may be recognized as a subgenus of *Pangasius* with *P. pleurotaenia* (senior synonym of *P. cultratus*) the only species.

The characters given by Chang and Wu (1965:13) in their diagnosis of *Sinopangasius* are all found in *Pangasius*, including the postpelvic abdominal keel. Such a keel, although not previously reported, occurs in all or almost all species of *Pangasius*, including *P. pangasius*. We have not found any characters that distinguish *Sinopangasius* from *Pangasius*.

Characters useful for distinguishing species of *Pangasius*

Head shape (Fig. 1).—Familiarity with head shape is useful in identifying species of *Pangasius*, but the often subtle differences are difficult to describe or even to convey in drawings, and there is much individual as well as ontogenetic variation. At least three species, *P. pangasius*, *P. conchophilus*, and *P. nasutus*, have pointed snouts in juveniles and subadults. In specimens over 30 cm, however, the snout is not pointed, but broadly rounded or truncate. A pointed snout may occur in juveniles and subadults of some additional species of which we have examined only larger specimens, e.g. *P. krempfi*. A very broad, rounded or slightly truncate head is characteristic of *P. sanitwongsei*. A moderately broad, rounded head is characteristic of *P. larnaudii*, and a relatively narrow, slightly pointed, truncate, or rounded head of *P. bocourti* and *P. djambal*. The head shape of the latter two species is very similar and unlike that of other species. *Pangasius macronema* has a very narrow head unlike that of any other *Pangasius*. A moderately broad truncate head (or snout), pointed in lateral view, is characteristic of *P. gigas* and *P. hypophthalmus*.

Mouth.—Species of *Pangasius* differ markedly in jaw position and size and shape of mouth. Three mouth types can be distinguished on the basis of jaw length: terminal, subterminal, and inferior. A terminal mouth occurs in only two species, *P. gigas* and *P. hypophthalmus*. The upper and lower jaws are very nearly equal. The anteriormost part of the upper jaw projects slightly in front of the lower, but this part is very narrow, much less thick than in other species. When the jaws are closed, the tooth band of the upper jaw is entirely covered by the lower jaw, a condition not found in other *Pangasius*. In most species, including *P. bocourti*, *P. conchophilus*, *P. djambal*, *P. krempfi*, and *P. macronema*, the tooth band of the upper jaw is largely or at least partly exposed when the mouth is closed, and the upper jaw and snout definitely project in front of the lower jaw, so the mouth may be described as subterminal. In one species, *P. nasutus*, the tooth band of the upper jaw is entirely exposed and the snout and upper jaw project so strongly that the mouth may be described as inferior.

Another distinction involves shape of ventral outline of lower jaw. In some species (*P. pangasius*, *P. bocourti*, *P. conchophilus*) it may be slightly rounded or curved, so that the mouth opening is nearly transverse, while in others it may be broadly rounded (*P. sanitwongsei*) or angulated (*P. macronema*, *P. micronema*, *P. pleurotaenia*, *P. polyuranodon*). These differences may be partially quantified by measuring the angle formed between the tip (symphysis) and both corners (ricti) of the lower jaw.

Mouth width also differs. It is greatest in *P. sanitwongsei*, least in *P. macronema* and *P. pleurotaenia*. This is most readily quantified as the proportion of mouth width either as times in or percent of standard length.

Palatal tooth bands (Fig. 2).—The palatal toothbands provide very useful distinctions among species of *Pangasius*. The primitive situation, commonly found in Bagridae, Ariidae, and many other catfish families, presumably is to have separate palatine and vomerine bands on each side, as occurs in *P. pangasius*, *P. macronema*, and *P. micronema*. In the latter two species the four toothplates are relatively

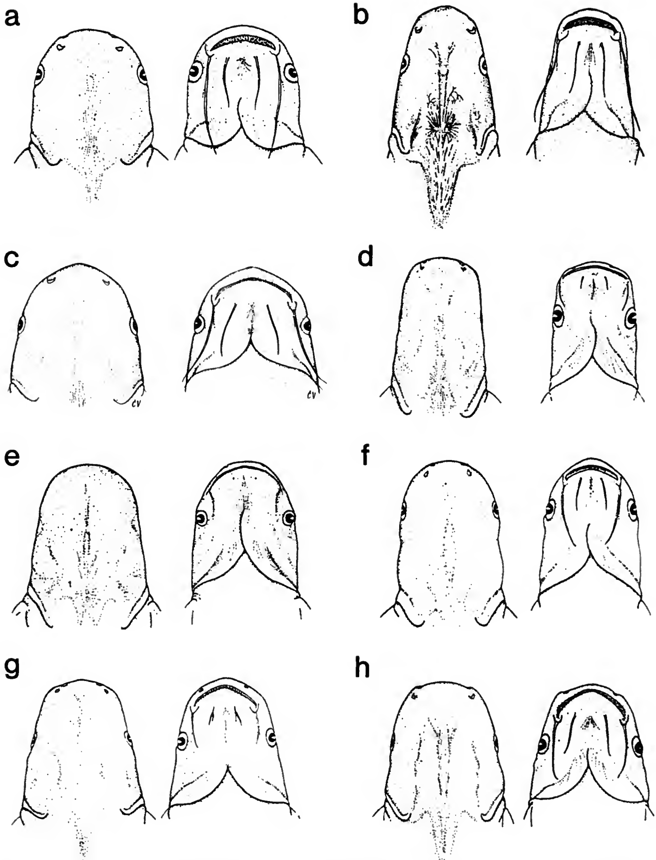

Fig. 1. Heads of *Pangasius* and *Helicophagus* (dorsal and ventral views): **a**, *P. bocourti*, 220 mm SL, Nongkhai; **b**, *P. conchophilus*, 240 mm, Nongkhai (holotype); **c**, *P. djambal*, 650 mm, Sintang; **d**, *P. gigas*, 250 mm, artifically reared; **e**, *P. gigas*, 565 mm, artifically reared; **f**, *P. hypophthalmus*, 216 mm, Pathumthani; **g**, *P. krempfi*, 538 mm, Nongkhai; **h**, *P. larnaudii*, 206 mm, Nongkhai.

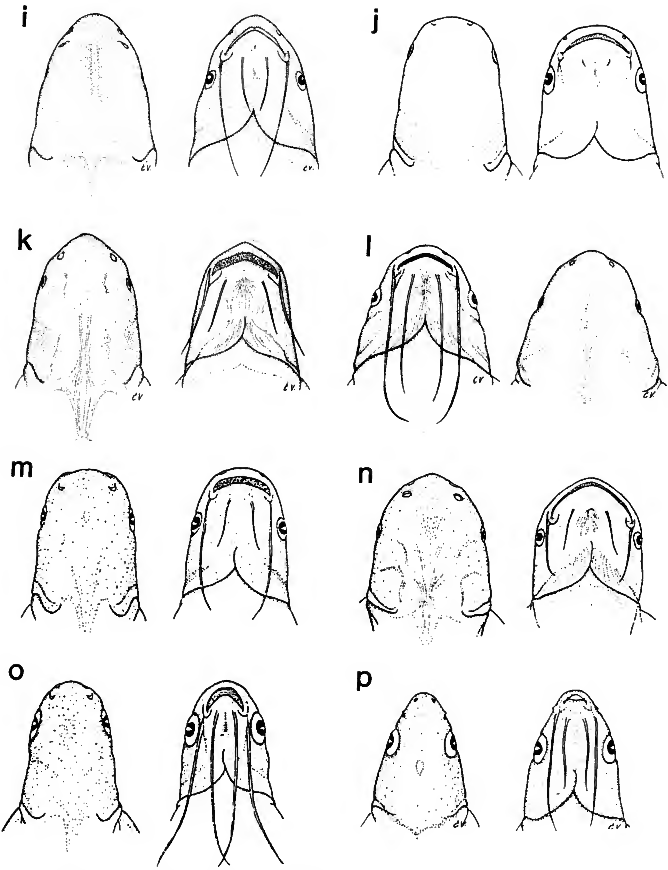

Fig. 1 (continued): **i**, *P. lithostoma*, 270 mm, Sintang; **j**, *P. micronema*, 128 mm, Kemarat; **k**, *P. nasutus*, 225 mm, Sintang; **l**, *P. pangasius*, 160 mm, Meghna River; **m**, *P. polyuranodon*, 219 mm, Ayutthaya; n, *P. sanitwongsei*, 129 mm, Mukdahan; **o**, *P. macronema*, 185 mm, Nongkhai; **p**, *H. waandersii*, 244 mm, Nan River, Uttaradit.

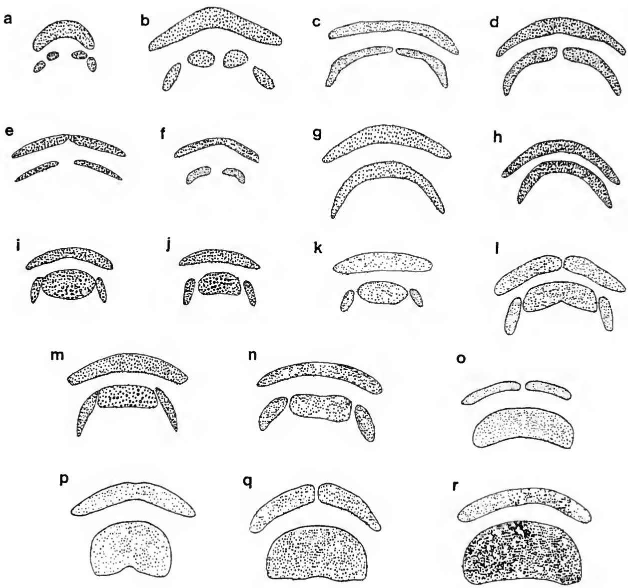

Fig. 2. Maxillary and palatal dentition of *Pangasius*: **a**, *P. macronema*, 185 mm SL, Nongkhai; **b**, *P. micronema*, 430 mm, Nongkhai; **c**, *P. pangasius*, 261 mm, Rangoon; **d**, *P. larnaudii*, 270 mm, Chao Phrya; **e**, *P. hypophthalmus*, 216 mm, Pathumtani; **f**, *P. pleurotaenia*, 211 mm, Nakorn Sawan; **g**, *P. krempfi*, 538 mm, Nongkhai; **h**, *P. sanitwongsei*, 179 mm, Mukdahan; **i**, *P. polyuranodon*, 219 mm, Ayutthaya; **j**, *P. conchophilus*, 240 mm, Nongkhai; **k**, *P. myanmar*, 230 mm, Rangoon; l, *P. nasutus*, 215 mm, Kapuas; **m**, *P. bocourti*, 245 mm, Nongkhai; **n**, *P. djambal*, 200 mm, Brantas; **o**, *P. humeralis*, 215 mm, Kapuas; **p**, *P. kinabatanganensis*, 224 mm, Kinabatangan; **q**, *P. lithostoma*, 214 mm, Kapuas; **r**, *P. nieuwenhuisii*, 400 mm, Mahakam (not drawn to scale).

small, round, and widely separated. In *P. pangasius*, however, they are elongate, curved, and related close-set, the whole forming a functionally single broadly curved toothplate, although the four plates are all clearly separate.

In *P. larnaudii* and *P. hypophthalmus*, the palatine and vomerine plates of each side are more or less perfectly joined into a single curved toothplate, but the vomerine portions of each side are more or less widely separated at the midline. In *P. krempfi* and *P. sanitwongsei* the palatine and vomerine tooth plates form a virtually uninterrupted broad, strongly curved, palatal tooth band. *Pangasius myanma* and *P. polyuranodon* have a more or less large, nearly square vomerine toothplate, with smaller but

discrete palatine tooth bands. *Pangasius bocourti* and *P. djambal* have a much wider median vomerine toothplate with large palatine plates juxtaposed to it. Finally, the endemic Bornean species *P. humeralis*, *P. kinabatanganensis*, *P. lithostoma*, and *P. nieuwenhuisii* have a single enormous median palatal toothplate. Whether this is formed exclusively from vomerine toothplates or represents palatine and vomerine plates combined presumably could be determined most readily by examination of smaller specimens than have been available to us.

Gill rakers (Table 2).—We found few previously published counts of gill rakers in *Pangasius*. These are helpful in recognizing and defining several species, such as *P. bocourti* and *P. djambal*. The total number of rakers on the first gill arch ranges from 12 to 46. Species may be categorized as having low, intermediate, or high counts based on the number of rakers being typically less than 20, between 20 and 30, or more than 30. Species with low counts include *P. larnaudii* (range 12-16), *P. pleurotaenia* (14-18), *P. micronema* (13-24), *P. conchophilus* (15-19), *P. sanitwongsei* (16-21), and *P. nasutus* (17-21). Intermediate counts occur in *P. polyuranodon* (20-29), *P. krempfi* (19-20), *P. humeralis* (19-22), *P. lithostoma* (22-26), *P. pangasius* (23-28), and *P. djambal* (24-35). Species with high counts include *P. bocourti*, in which the rakers are relatively short (36-46), and *P. macronema*, in which they are longer than in any other species (36-45).

The condition of the gill rakers deserves special mention in two species. In the giant species *P. gigas*, they are absent in specimens over 500 mm standard length, and in smaller specimens very small or rudimentary. The maximum number of rakers on the unusally short upper limb of the first gill arch, 3-4, is much less than that observed in other species. Finally, in *P. hypophthalmus* the gill rakers are not of regularly increasing or decreasing size along the arch as in all other species, but smaller rakers alternate with large ones of normal size. The small rakers are included in our counts for *P. hypophthalmus*.

Data on gill raker counts is generally consistent throughout the range of species recognized in this revision. For example, *P. macronema* from Borneo have 37-45 rakers on first arch and those from Thailand 36-44. Two relatively interesting instances of variation in gill raker counts involve *P. djambal* and *P. micronema*. In *P. djambal* we found gill raker counts of 24-26 and 30-35. This may be related to the small sample size (n=14), since low counts and high counts occur in specimens from Java and from Borneo. Another perhaps more puzzling example concerns *P. micronema*, in which 4 specimens from Java have 23-26 rakers, and 39 specimens from all other localities have only 13-21.

Filamentous fin extensions.—Most of the species, including *P. pangasius*, lack filamentous fin extensions. These are most notable in the giant species *P. santiwongsei*, in juveniles and adults of which the last unbranched ray of the dorsal and anal fins and the outermost pectoral and pelvic fin rays may all be greatly elongated (frequently, however, the elongate portions of the pectoral and particularly anal fins are missing, that of the anal fin possibly lost by abrasion in many individuals). *Pangasius larnaudii* has similar but shorter extensions of the same fins. Males of *Pangasius macronema* and *P. polyuranodon* sometimes have filamentous extensions of the dorsal and pectoral fins but not of the pelvic and anal, while males of *P. krempfi* have filamentous extensions of the dorsal and pelvic fins but not of the pectoral and anal. None of the species has elongate extensions of caudal fin rays.

Swimbladder (Fig. 3).—The swimbladder is useful in charcterizing species. It may be confined to the abdominal cavity, or extend for some distance above the base of the anal fin, or even, in *P. krempfi*, to the caudal fin base. And it may consist of a single chamber, two chambers, three chambers, or a whole series of chambers. In all species the walls of the chamber are relatively rigid, and its interior is stiffened by more or less highly developed fibrous struts.

A single swim bladder chamber occurs in *P. gigas* and *P. hypophthalmus*; in *P. gigas* it is

Table 2. Frequency distributions of gill raker counts (total rakers on first arch) in species of *Pangasius*.

species	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
bocourti	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	1	1	1	1	-	-	3
conchophilus	1	2	1	5	3	7	4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
djambal	-	-	-	-	-	-	-	-	-	-	-	1	2	3	-	-	-	1	1	1	2	2	1	-	-	-	-	-	-	-	-	-	-	-
gigas (juvenile)	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
humeralis	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
hypophthalmus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	1	2	-	-	1	2	-	-	-	-	-	-	-	-
kinabatanganensis	-	-	-	-	-	-	-	-	-	1	1	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
krempfi	-	-	-	-	-	-	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
larnaudii	1	2	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
lithostoma	-	-	-	-	-	-	-	-	-	1	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
macronema	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	3	5	4	7	5	5	4	2	2	-
micronema	4	2	3	2	9	4	9	4	2	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
myanmar	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
nasutus	-	-	-	-	1	1	1	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
nieuwenhuisii	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
pangasius	-	-	-	-	-	-	-	-	-	-	3	7	16	9	5	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
pleurotaenia	-	1	7	5	9	5	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
polyuranodon	-	-	-	-	-	-	2	5	1	2	2	7	1	3	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
sanitwongsei	-	1	1	2	3	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

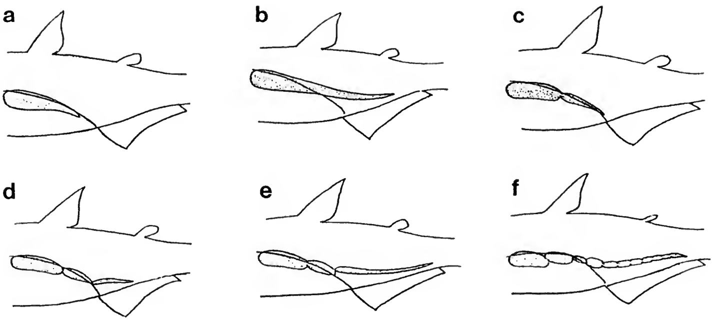

Fig. 3. Swimbladder in *Pangasius* (diagrammatic): **a**, single chamber confined to abdomen (*P. gigas* only); **b**, single chamber extending posteriorly above anal fin (*P. hypophthalmus* only); **c**, two chambers confined to abdomen (*P. bocourti*, *P. conchophilus*, *P. djambal*, *P. humeralis*, *P. kinabatanganensis*, *P. lithostoma*, *P. myanmar*, *P. nasutus*, some *P. pangasius*, *P. sanitwongsei*) (in some *P. pangasius* second chamber extends posteriorly above anterior third of anal fin); **d**, three chambers, posterior extending over anterior third of anal fin (*P. larnaudii*); **e**, three chambers, posterior extending to or beyond end of anal fin (*P. krempfi*, *P. macronema*, *P. micronema*, *P. polyuranodon*); **f**, two or three chambers confined to abdomen and a variable number of irregular small chambers extending to end of anal fin (*P. pleurotaenia* only).

confined to the abdominal cavity, in *P. hypophthalmus* it extends beyond the cavity dorsal to above the posterior half of the anal fin base. *Pangasius bocourti*, *P. conchophilus*, and *P. sanitwongsei* have a two-chambered swimbladder confined to the abdomen. *Pangasius krempfi*, *P. macronemus*, *P. micronemus*, and *P. polyuranodon* have a three-chambered swimbladder, with the last chamber extending over the anterior half of the anal fin base, to the end of the anal fin base, or even beyond to the base of the caudal fin (*P. krempfi*). Finally, *P. pleurotaenia* has a three-chambered swimbladder with the first two chambers confined to the abdomen, and the third, extending to or nearly to end of anal fin base, divided into as many as 6 or 8 chambers or segments.

Coloration.—In all species of *Pangasius* the dorsal parts are dull grey, slate, or near black, or iridescent blue, bluish green, green, or bronze; the ventral parts are usually white, and the fins most often dusky. Several species lack distinctive color pattern or marks on the body and fins, including *P. pangasius*, *P. conchophilus*, *P. krempfi*, *P. micronema*, *P. nasutus*, *P. polyuranodon*, and *P. gigas* and *P. hypo-phthalmus* over 40 or 50 cm. In *P. conchophilus* dorsal color in fresh specimens is variable. At Ubol Ratchatani numerous individuals observed in June-July 1985 and, December 1988 and May 1989 were iridescent pale green. Fresh specimens observed at Prachinburi in March 1989 were dull grey, those at Singburi in April 1989 bronze. The single specimen of *P. krempfi* observed fresh had sky blue dorsal coloration.

Many, perhaps all, species of *Pangasius* juveniles have a very distinctive striped color pattern. In some species it involves only two dark stripes, a dorsal stripe extending the body length, and a short downward sloped stripe separating from the dorsal stripe behind the

pectoral fin. Other species have three dark stripes, a dorsal longitudinal stripe extending the body length, a midlateral longitudinal stripe extending the body length, and a short downward sloped stripe separating from the midlateral stripe just behind the head and above the pectoral fin base. In several species this "juvenile coloration" is retained through life, e.g. *P. macronema* and *P. pleurotaenia*, while in *P. gigas* and *P. hypophthalmus* it is retained in specimens to 20 or 30 cm but entirely absent in those over 50 cm.

Several species have submarginal dark stripes on the caudal fin lobes, e.g. *P. larnaudii* and *P. pleurotaenia* throughout life, juveniles of *P. bocourti*. A stripe in the middle of the anal fin is seen in *P. hypophthalmus* under 30 cm and in the only two specimens of *P. djambal* we have examined with well preserved color pattern. Black pectoral and dorsal fins are characteristic of *P. humeralis*, and black pectoral fins occur in some specimens of *P. micronema*. A few species have unique color features, such as the large black humeral spot in juveniles and adults of both sexes of *P. larnaudii*.

Vertebral counts (Table 3).—We find no previously published vertebral counts for *Pangasius* except for four species from Borneo (Roberts 1989). Total vertebrae range from 39-52. Most species have 45 or fewer vertebrae, while a few have 48 or more. The lowest vertebral counts are found in *P. conchophilus* (39-44), the highest in *P. krempfi* (48-52), *P. lithostoma* (51), and *P. sanitwongsei* (50-52). In catfishes generally, within a genus the lowest vertebral counts occur in the smallest species, and the highest counts in the largest (and fastest growing) species. This tendency appears to hold in *Pangasius* but is not very marked. *Pangasius conchophilus*, attaining standard lengths to 1 m, has the lowest vertebral counts in the genus. The smallest species, *P. macronema*, attaining only 20 cm, has the next lowest counts (41-45). The giant species *P. sanitwongsei* has very high counts, as expected, but the only two radiographed specimens of the still larger species *P. gigas* have a relatively low count (48). One of these specimens was pond-reared; the other (holotype *P. paucidens*) is the only known wild (i.e. not artifically reproduced) specimen of *P. gigas* with an intact vertebral column. Several other small specimens of pond-reared *P. gigas* were cleared and stained; these have even fewer vertebrae, but exhibit marked vertebral column teratology including centric fusions, and apparently anomalous counts (45-46) not included in Table 3.

Vertebral counts have greater utility as a diagnostic character when abdominal and caudal vertebrae are tabulated separately (Table 3). Three species have relatively low counts of abdominal vertebrae, *P. hypophthalmus* (15-16), *P. macronema* (14-16) and *P. pleurotaenia* (15-17), while one species, *P. sanitwongsei*, has exceptionally high counts (21-23). *Pangasius polyuranodon*, which has the most elongate body of any species of *Pangasius*, is noteworthy for having relatively few abdominal vertebrae 16-19) and many caudal (28-32); its abdomen is proportionately short. The least difference between abdominal and caudal vertebral counts occurs in *P. bocourti* (19-23 vs. 25-27); its abdomen is proportionately elongate.

In most species we find rather similar vertebral counts throughout the range. Thus in *P. macronema*, which has a markedly disjunct distribution, specimens from Thailand have 42-45 vertebrae, and from Borneo 41-43. In *P. conchophilus*, 7 specimens from Chao Phraya and Bangapakong basins have only 39-41 vertebrae (lowest vertebral counts observed in *Pangasius*), while 17 specimens from the Mekong basin have slightly higher counts, 42-44. *Pangasius micronema* from the Kinabatangan basin in northeastern Borneo (type series of *P. tubbi*) have slightly higher counts than specimens from other areas (discussed under *P. micronema*).

Total vertebral counts include the four anteriormost vertebrae associated with the Weberian apparatus, and the hypural fan centrum (counted as a single vertebra). The four anteriormost vertebrae are difficult to count on radiographs or even in cleared and stained specimens, as their centra may be partially

Table 3. Frequency distributions of vertebral counts in species of *Pangasius*.

	Abdominal										Caudal										Total													
species	14	15	16	17	18	19	20	21	22	23	23	24	25	26	27	28	29	30	31	32	39	40	41	42	43	44	45	46	47	48	49	50	51	52
bocourti	-	-	-	-	-	1	3	3	-	-	-	-	1	2	5	-	-	-	-	-	-	-	-	-	-	-	1	1	3	2	1	-	-	-
conchophilus	-	1	3	9	11	-	-	-	-	-	1	8	14	1	-	-	-	-	-	-	1	4	2	8	8	1	-	-	-	-	-	-	-	-
djambal	-	-	-	-	2	9	-	-	-	-	-	-	-	2	8	1	-	-	-	-	-	-	-	-	-	-	3	8	-	-	-	-	-	-
gigas	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
humeralis	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-
hypophthalmus	-	1	7	-	-	-	-	-	-	-	-	-	3	4	1	-	-	-	-	-	-	-	1	2	4	1	-	-	-	-	-	-	-	-
kinabatanganensis	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1	-
krempfi	-	-	-	-	-	-	1	1	2	-	-	-	-	1	1	-	1	-	1	-	-	-	-	-	-	-	-	-	1	2	-	-	-	1
larnaudii	-	-	-	3	1	1	1	-	-	-	-	-	1	3	2	-	-	-	-	-	-	-	-	-	2	2	1	1	-	-	-	-	-	-
lithostoma	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
macronema	17	9	1	-	-	-	-	-	-	-	-	-	-	-	4	12	7	3	-	-	-	-	2	10	6	6	1	-	-	-	-	-	-	-
micronema	-	-	1	4	14	12	1	-	-	-	-	-	-	6	17	2	1	4	2	-	-	-	-	-	-	3	10	12	4	3	-	-	-	-
myanmar	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-
nasutus	-	-	-	1	4	5	1	-	-	-	-	-	1	8	2	-	-	-	-	-	-	-	-	-	1	8	2	-	-	-	-	-	-	-
nieuwenhuisii	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
pangasius	-	-	-	16	20	4	-	-	-	-	-	-	17	19	4	-	-	-	-	-	-	-	-	5	20	11	4	-	-	-	-	-	-	-
pleurotaenia	-	3	18	1	-	-	-	-	-	-	-	-	-	-	4	13	3	1	-	-	-	-	-	-	5	12	5	-	-	-	-	-	-	-
polyuranodon	-	-	2	4	4	1	-	-	-	-	-	-	-	-	-	3	1	6	1	1	-	-	-	-	-	-	1	3	3	2	1	1	-	-
sanitwongsei	-	-	-	-	-	-	-	1	8	1	-	-	-	-	-	2	6	2	-	-	-	-	-	-	-	-	-	-	-	-	-	2	6	2

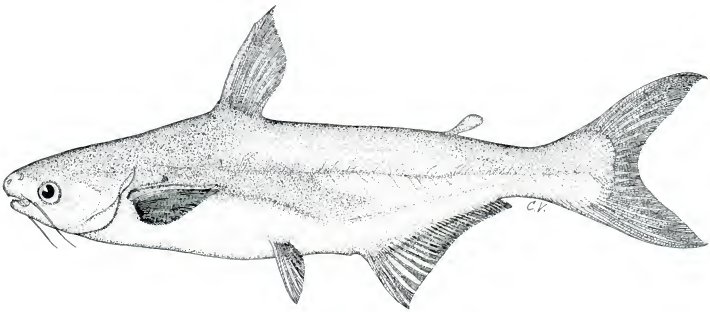

Fig. 4. *Pangasius bocourti*, 220 mm SL; Mekong basin, Nongkhai (NIFI 2272).

fused and otherwise modified. The fourth centra is usually very elongate. In practice, counts on radiographs are begun by identifying the fifth vertebra, which in *Pangasius* usually has a normal-sized separate centrum and bears the first pair of ribs. The first caudal vertebra is identified as the first vertebra having hemal process with its tip posterior to proximal end of anteriormost anal fin pterygiophore(s). Such a definition works well (i.e. permits repetition of counts give or take one vertebra) not only for Pangasiidae, but for many other catfish and teleost families (see Roberts 1989, and references cited therein).

KEYS TO SPECIES OF *PANGASIUS*

In order to facilitate identification, we present two keys, one to species found in Indo-China and Thailand, and one to species found in Malaysia and Indonesia. *Pangasius polyuranodon* generally has fewer anal fin rays in Thailand and Indo-China than in Malaysia and Indonesia; this difference is reflected in the keys. As only a single species occurs in the Indian subcontinent (*P. pangasius*) and only two in Burma (*P. pangasius*, *P. myanmar*), no keys are given for these areas.

Pangasius bocourti Sauvage
Figs. 1a, 2m, 4

Pangasius bocourti Sauvage, 1880:229 (type locality Phnom-Penh); Sauvage, 1881:170, pl. 8, fig. 4 (head dorsal view); Kottelat, 1984:812.

Pangasius altifrons Durand, 1940:23, pl. 5. (type locality Tonle-Sap).

Material examined.—MNHN 9528, 265 mm, Phnom-Penh, Harmand (holotype *P. bocourti*); NIFI 4438, 205 mm, Chainat; ZSM/CMK 5999, 148 mm, Ayuttaya, May 1988?; NIFI 2245, 200 mm, Nongkhai; NIFI 2272, 220 mm, Nongkhai; NIFI 2276, 430 mm, Nongkhai; CAS 67195, 138 mm, Mekong R. at Bung Kla (140 km N of Nakorn Phanom), T. R. Roberts, 7 July 1985; NIFI 2292, 8:54.5-92.6 mm, That Phanom; NIFI 2246, 4:82.0-108 mm, Mukdaharn; CAS 67196, 159 mm, Khong Chiam market, T. R. Roberts, May 1989.

Notes on type specimens.—The holotype of *P. bocourti*, in poor condition, has 15+28=43 gill rakers on first gill arch. A search for the holotype of *P. altifrons* in the MNHN in May 1989, with the help of M.-L. Bauchot, was unsuccessful, and it is presumed lost. Our identification of this nominal species as *P. bocourti* is based on Durand's figures (including that of palatal dentition). No gill raker count was given.

Key to *Pangasius* of Indo-China and Thailand

1a. Abdomen entirely keeled, anal fin rays 39- 46 .... ***P. pleurotaenia***
1b. Abdomen rounded anterior to pelvic fins; anal fin rays 26-37............................... **2**

2a. Pelvic fin rays 8 (occasionally 9); mouth terminal; swimbladder with single lobe **3**
2b. Pelvic fin rays 6; mouth subterminal; swimbladder with two or three lobes **4**

3a. Gill rakers very small, rudimentary, or absent; swim-bladder confined to abdomen; head length more than 29% SL; mouth width more than 12% SL .... ***P. gigas***
3b. Gill rakers normally developed; swimbladder usually extending posteriorly beyond abdomen dorsal to anal fin base; head length less than 27% SL; mouth width less than 10% SL .... ***P. hypophthalmus***

4a. Swimbladder with two lobes **5**
4b. Swimbladder with three lobes **8**

5a. Black humeral spot .... ***P. larnaudii***
5b. No black humeral spot **6**

6a. Snout slightly to noticeably pointed; caudal peduncle relatively slender, depth less than 6.5% SL; abdominal stripe absent .... ***P. conchophilus***
6b. Snout rounded; caudal peduncle depth more than 7% SL; abdominal stripe present **7**

7a. Mouth very wide, width more than 17% SL; palatine and vomerine teeth forming a wide, nearly continuous, single palatal tooth band; dorsal, pectoral, pelvic and anal fins with filamentous extensions; gill rakers on first gill arch 16-21 .... ***P. sanitwongsei***
7b. Mouth narrower, width less than 10% SL; palatal teeth with median vomerine and lateral palatine tooth bands; fins without filamentous extensions; gill rakers 40-46 .... ***P. bocourti***

8a. Angle of lower jaw less than 90 degrees; midlateral and abdominal stripes present; barbels reaching base of pectoral fin; gill rakers more than 37 .... ***P. macronema***
8b. Angle of lower jaw more than 100 degrees; midlateral and abdominal stripes absent; gill rakers less than 25 .... **9**

9a. Snout relatively elongate; palatal teeth in two crescentic patches; adipose fin width more than 1.9% SL .... ***P. krempfi***
9b. Snout relatively short; palatal teeth in three or four patches; adipose fin minute, width less than 1.3% SL **10**

10a. Maxillary barbels extending posteriorly to gill opening; anal fin rays 32-36; a large median vomerine tooth patch and very small palatine tooth patch .... ***P. polyuranodon***
10b. Maxillary barbels only extending to or slightly beyond posterior margin of eye; anal fin rays 28-32; two palatine and two vomerine tooth patches .... ***P. micronema***

Key to *Pangasius* of Malaysia and Indonesia

1a. Palatal teeth consisting of a single large tooth patch (species known only from Borneo) **2**
1b. Palatal teeth consisting of palatine and vomerine tooth patches **5**

2a. Pectoral gland greatly enlarged; humeral spine extending two-thirds to three-fourths of distance to end of pectoral fin spine **3**
2b. Pectoral gland not greatly enlarged; humeral spine extending one-half or less distance to end of pectoral fin spine **4**

3a. Pectoral fin black; snout rounded . . . . **P. humeralis**
3b. Pectoral fin dusky or plain; snout pointed . . . . **P. nieuwenhuisii**

4a. Palatal tooth patch convex projecting strongly down from roof of mouth; anal fin rays 40-41 . . **P. lithostoma**
4b. Palatal tooth patch relatively flat, not projecting strongly down from roof of mouth; anal fin rays 27-29 . . . . **P. kinabatanganensis**

5a. Snout strongly projecting; mouth inferior; tooth band of upper jaw entirely exposed when mouth closed . . . . **P. nasutus**
5b. Snout moderately or slightly projecting; mouth subterminal; tooth band of upper jaw partially or largely exposed when mouth closed **6**

6a. Gill rakers elongate, 37-45 on first gill arch; midlateral and abdominal stripes well defined, separated at level of pectoral fin origin . . . . **P. macronema**
6b. Gill rakers short or moderately long, less than 37 on first gill arch; midlateral and abdominal stripes absent, or poorly defined and separated posterior to end of pectoral spine **7**
7a. Anal fin rays 28-32 . . . . **8**
7b. Anal fin rays 32-44 . . . . **P. polyuranodon**

8a. Palatal teeth with two palatine patches and a greatly enlarged median vomerine patch; maxillary barbels extending to gill opening; gill rakers on first gill arch 24-35 . . . . **P. djambal**
8b. Palatal teeth with two palatine and two vomerine patches; maxillary barbel extending to or somewhat beyond posterior border of eye; gill rakers on first gill arch 13-26 . . . . **P. micronema**

Comparative description.—*Pangasius bocourti* differs from all other species of *Pangasius*, except *P. macronema*, in its numerous gill rakers, 36-46 on first gill arch (Table 2). It differs from *P. macronema* in having a broader, more rounded head, gill rakers relatively short rather than very elongate, body with two stripes instead of three, submarginal stripes usually present on both lobes of caudal fin or on dorsal lobe, rather than absent, and in other respects. Despite the shared character of high raker counts, the two species evidently are not closely related. *Pangasius bocourti* is most similar to the Indonesian species *P. djambal*, from which it differs in having more numerous gill rakers; the total number of vertebrae is similar in the two species, but *P. bocourti* tends to have a higher ratio of abdominal to caudal vertebrae than *P. bocourti* (Table 3). There may also be differences in coloration, but not enough is known about coloration in *P. djambal*.

Distribution.—*Pangasius bocourti* occurs in the Mekong and Chao Phraya basins.

Pangasius conchophilus new species
Figs. 1b, 2j, 5

Pangasius nasutus. Smith, 1945:362 (Menam Chao Phraya).

Holotype.—NIFI 2227, 240 mm, Thabo, Nongkhai prov.

Paratypes.—CAS 67197, 183 mm, Ayutthaya market, T. R. Roberts, 5-7 April 1989; NIFI 437, 2:139-154 mm, Ayutthaya; NIFI 454, 255 mm, Chainat; CAS 67515, 316 mm, Suphanburi market, T. R. Roberts, 7-8 Feb. 1989; CAS 67200, 575 mm, Singburi market, T. R. Roberts, 9 April 1989; KUMF 1043, 115 mm, Lopburi R.; KUMF 1042, 134 mm, Bangkok; CAS 67198, 5:138-196 mm, Bangpakong R. near Prachinburi, T. R. Roberts, 22 March 1989; NIFI 443, 177 mm, Nongkhai; NIFI 2243, 175 mm, Nongkhai; NIFI 2227, 240 mm, Thabo, Nongkhai prov.; CAS 67216, 2:95.1-95.7 mm, Mekong R. at Bung Kla, T. R. Roberts, 7 July 1985; ZSM/CMK 5095, 5:141-258 mm, That Phanom market, M. Kottelat, 18 March 1985; NIFI 2251, 19:45.5-76.5 mm, Nakorn Phanom; ZSM/CMK 5110, 277 mm, Mukdahan prov., Amphur Don Than market, M. Kottelat, 18 March 1985; NIFI 447, 3:124-225 mm, Kemarat; CAS 67199, 10:83.3-280 mm, Ubol

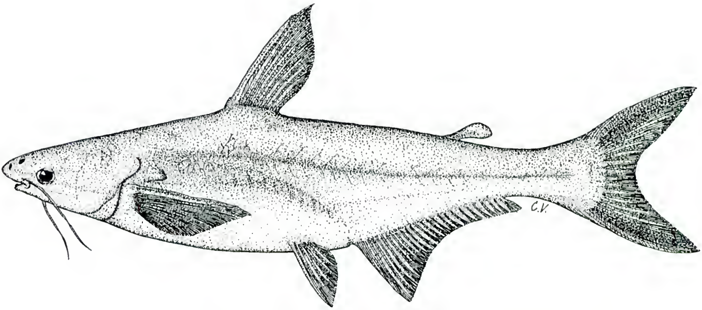

Fig. 5. *Pangasius conchophilus*, 240 mm SL; Mekong basin, Nongkhai (NIFI 2227, holotype).

Ratchatani market, T. R. Roberts, 28 June-2 July 1985; NRM A88/1988.989.3003-05, 3:198-294 mm, Mekong R. at Pakse, 1987 or 1988; ZSM/CMK 4807, 62.8 mm, Snoc Trou, Prek Tasom, F. d'Aubenton, June 1961.

Comparative description.—*Pangasius conchophilus* differs from all other *Pangasius* in Thailand and Indo-China except *P. bocourti* and *P. polyuranodon* in having a large median vomerine toothplate, and in all the Thai and Indo-Chinese species so far as known in having a pointed snout in juveniles. From the Malaysian and Indonesian species *P. nasutus*, with which it has been misidentified, *P. conchophilus* differs in having relatively larger eyes in juveniles and subadults; less pointed snout in juveniles and more or less truncate rather than broadly rounded snout in large adults; and in having a subterminal rather than terminal mouth, with a less strongly projecting snout. Gill rakers on first gill arch 15-19; anal fin rays 25-30; vertebrae 39-44. Direct comparison of the 575 mm paratype of *P. conchophilus* (obtained specifically for this purpose) with the 558 mm *P. nasutus* from Perak (holotype *P. ponderosus*) reveals that the latter has a more strongly projecting and rounded snout, with a decidedly more inferior mouth. The difference in eye size, pronounced in specimens below 300 mm, is not evident: in the 575 mm *P. conchophilus*, the diameter of exposed portion of eye is 10.7 mm, or 54 times in SL, compared to 48-52 in the two large specimens of *P. nasutus*.

Food habits.—Juveniles feed on prawns and insects, subadults and adults on prawns, insects, and particularly molluscs, with molluscs more predominant in stomach contents than in any other species of *Pangasius*. Snails and clams are invariably swallowed whole, i.e., without crushing the shells. Gluttony is particularly evident in this species. Among the numerous individuals examined in the field were many of 10-20 cm with abdomens and guts greatly distended by bivalves. Some juveniles of 2-4 cm were similarly distended by a whole large grasshopper. The grasshopper exoskeletons and larger clam shells may be evacuated rather than digested, since those examined by us from the guts of *P. conchophilus* are intact and show little or no sign of digestion. In individuals with abdomens and guts greatly distended the vent is often also distended. We suppose this is an adaptation to permit ejection of large undigested hard parts.

Although the mollusc-eating habits of the pangasiid genus *Helicophagus* have been rec-

ognized since its description, significant molluscivory has not been reported until now in any species of *Pangasius*. Of 22 specimens (138-270 mm) of *P. conchophilus* radiographed in order to obtain vertebral counts, 15 (68%) contain molluscs: gastropods or snails in 10, bivalves or clams in 4, and both in 1. A specimen of 183 mm from Ayutthaya contains some 60 snails of about 5 mm. Four specimens 165-195 mm from Mun R. at Khong Chiam each contain some 10-20 20 clams of 8-10 mm. Molluscs do not appear to be a very important dietary item in any other species of *Pangasius*. Of 228 radiographed specimens, representing all other species in the genus except *P. nieuwenhuisii* (probably vegetarian), molluscs are evident in only five: two *P. bocourti* (few large snails and clams), two *P. polyuranodon* (small snails), and one *P. pangasius* (many large clams).

Potential use in aquaculture.—*Pangasius conchophilus* is a large, apparently fast growing species, perhaps the most important *Pangasius* in markets of the Chao Phraya and Mekong in Thailand. It might be valuable in aquaculture, possibly in mixed culture with *P. hypophthalmus*, in ponds populated by molluscs.

Etymology.—The name *conchophilus*, a combination of the Latin *concho* (shell) and *philus* (loving), refers to the pronounced molluscivory of this species.

Distribution.—*Pangasius conchophilus* occurs in the Mekong, Bangpakong, and Chao Phraya basins.

Pangasius djambal Bleeker
Figs. 1c, 2n

Pangasius djambal Bleeker, 1846:290 (type locality Batavia, in fluviis); Bleeker, 1862b:73, pl. 81 (Java).

Pangasius pangasius. Weber and de Beaufort, 1913:256 (in part).

Material examined.—RMNH 6854, 369 mm, Bleeker collection, presumably from Java (neotype); RMNH 31192 (ex RMNH 6854), 6:112-210 mm, Bleeker collection; RMNH 8069, 215 mm, Batavia, Bleeker collection, 1852; BMNH 1863.12.11.81, 397 mm, Java, Bleeker collection; UMMZ 155811, 253 mm, Batavia, Hardenberg and C. L. Hubbs, May 1929; ZMA 115.737, 2:156-200 mm, Java, Brantas R., Kali, G. J. Terviel, 1927; ZMA 115.740, 2:420-440 mm, Borneo, Sungei Sidalit, Mohari, 1912.

Designation of neotype.—No type specimen is indicated in the original description, and no primary type specimen has been designated subsequently. We designate RMNH 6854, a 369 mm specimen in excellent condition from Bleeker's collection, as neotype. It lacks locality data, but since Bleeker (1858:182, 1862:74) recorded the species only from Java, it presumably was collected there.

Comparative description.—*Pangasius djambal* has juveniles and adults with a rounded or somewhat truncate (never pointed) snout; palatal teeth in two palatine bands and a moderately large median vomerine patch (but vomerine patch usually clearly divided in two in juveniles); at least some specimens with a well marked color pattern on body and fins, including two stripes on body, a mid-anal fin stripe, and stripes on caudal fin lobes. It is very similar morphologically to *P. bocourti* from the Chao Phraya and Mekong basins, but differs in having only 24-35 rakers on first gill arch instead of 36-46.

Size.—Attains at least 60 cm standard length.

Distribution.—*Pangasius djambal* is known only from Java and Borneo. Bleeker (1858:182) reported it from Batavia, Krawang, Tjikao, and Parongkalong, all on the island of Java. The material examined represents all known localities for which specimens are available.

Pangasius gigas (Chevey)
Figs. 1d-e, 6, 7

Helicophagus hypophthalmus Sauvage, 1881:171 (partim: only the specimen 1 m long).

Pangasius [sp. undet.] Vaillant, in Pavie, 1904:457 (Cambodge, Laos).

Pangasianodon gigas Chevey, 1930:536 (type locality Cambodge).

Pangasius paucidens Fang and Chaux, 1949:344, fig. 6 (type locality Cambodge).

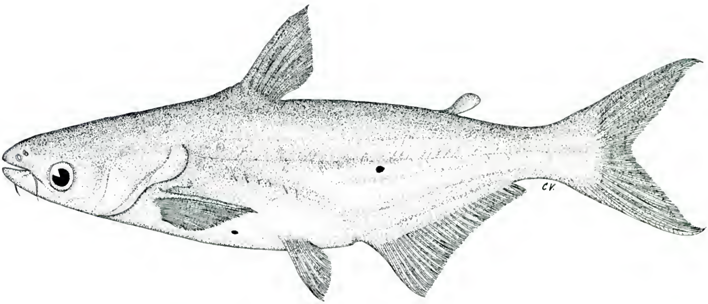

Fig. 6. *Pangasius gigas*, 282 mm SL; Chieng Rai, pond reared (NIFI 2259).

Material examined.—MNHN A.8832, 87 cm (stuffed, with glass eyes), Laos Siamois, Harmand, 1875 (paralectotype *Helicophagus* [=*Pangasius*] *hypophthalmus*); MNHN 1966.730, 347 mm, Cambodge (holotype *P. paucidens*); NIFI 1620-27, 8:20.0-55.0 mm, artificially reared at Chiang Rai; NIFI 2257-60, 2263, 34:64.0-565 mm, artifically reared at Chiang Rai; NIFI 2261, 160 cm, Nongkhai (skeleton); NIFI 2262, 200 cm, Chiengrai (skeleton).

Notes on type specimens.—The 347 mm specimen (holotype of *P. paucidens*) is perhaps the only whole alcohol-preserved specimen available in museum collections that was caught in the wild before the release of large numbers of artifically reared fry. It has no maxillary barbels; mandibular barbels 3-4 mm long; teeth of both jaws and palate absent; first gill arch with about five vestigial gill rakers on posterior part of lower limb (near angle of arch); lower limb extremely elongate, upper limb very rudimentary, without rakers; both pelvic fins with 9 rays; anal fin rays 35?; and vertebrae 20+28=48.

Comparative description.—*Pangasius gigas* differs from all other species of *Pangasius* in attaining a size of 3 m and 300 kg, and in loosing the oral teeth, gill rakers, and mandibular barbels at lengths of about 300 to 500 mm. From the other giant species, *P. sanitwongsei*, it differs in having a narrower head, no filamentous fin extensions, and in many other characters. It differs from all other species except *P. hypophthalmus* in having 8 (occasionally 9) instead of only 6 pelvic fin rays, and a terminal rather than subterminal or inferior mouth. *Pangasius gigas* differs from *P. hypophthalmus* in having a broader head and mouth (width of head 14.3-21.0 and of mouth 12.0-14.8% SL in *P. gigas*, versus 13.3-15.6 and 8.3-9.7% in *P. hypophthalmus*), and swim bladder confined to abdomen (rather than extending posteriorly above anal fin).

As mentioned by Chevey (1930:541), in large individuals the eye is situated partly or wholly below the level of the rictus of the jaws ("commissure labiale"), a condition not observed in *P. hypophthalmus* or any other species of *Pangasius*. In specimens less than 30 cm, however, the eye lies level with or above the level of the rictus, at the same position as in *P. hypophthalmus* and other species (Fumihito 1989:116). Lowering of the eye level with growth is known only in *P. gigas*.

A 76.3 mm cleared and stained specimen of *P. gigas* has 3+14 rakers on first gill arch. The five posteriormost rakers on the lower limb are smaller than those observed in any other species, but they are much larger than the more

anterior rakers on the lower limb and those on the upper limb, which are tiny or rudimentary. Perhaps the gill rakers of *P. gigas* at this size play no role in feeding and are truly vestigeal.

Although we have not tried to quantify the difference, in *P. gigas* the upper limbs of the gill arches are evidently shorter and the lower limbs more elongate than in any other species of *Pangasius*. Thus, in a 106 mm *P. gigas* the lower limb of the first gill arch is about 12 times longer than the upper limb. In *P. hypophthalmus* of comparable size the lower limb is only about 4 times longer than the upper. The proportions of the upper and lower limbs in other species are close to that observed in *P. hypophthalmus*.

Historical account.—The first published notice of the Mekong giant catfish is by Pavie (1904:455), whose account is reproduced here (our translation from the French):

> Among the fishes of this family of Silurides which Tirant has not studied, I have brought to the attention of Leon Vaillant by sending him the photographs reproduced herein, which by their considerable dimensions, as well as by their value, merit particular attention.
>
> This fish often exceeds a meter and a half in length. The Cambodians call it "Trey réach" (Royal Fish). They capture a large number at Pnom Penh, at the place known as Quatre-Bras, after the rainy season and the waters have returned to their normal level, when it ascends the Mekong, going to spawn in Lake Tali.
>
> At the time of its passage in Cambodia the trey réach is very fat; thus, in addition to the consumption of its flesh, considerable oil is extracted.
>
> When, having continued its voyage, it arrives at Luang Prabang in February, the fishermen wait for it, and when the first groups are seen, the fish swimming nearly at the surface of the water, a hundred canoes armed with long narrow nets bar their route, as they will do again on their return. The fisheries is thus carried on until June. The flesh is placed in brine and a kind of caviar prized throughout Laos is made of the eggs. Highly variable numbers are caught each year at Luang Prabang: in 1889, 1,400 individuals were captured, and in 1890, 6,000. A thousand also are taken each year in the pond of Dan Keo near Pak-Lay, when the water is drained off.
>
> The Laotians call it "Pla boek." They believe that only the females frequent the river and suppose that the males, with golden scales, never leave Lake Tali, where they await the females.
>
> According to the learned Professor of the Museum [Vaillant], "this is a catfish; the genus does not seem doubtful, it is a *Pangasius*. As to the species identity, that is more difficult. M. Sauvage, in his ichthyological fauna of Asia, cites seven species of which two are from Pnom-Penh: *P. pleurotaenia* and *P. bocourti*. These species are named after small individuals so that their pertinence is doubtful. One specimen, without locality nor certain donor, possessed by the Museum, seems to belong to *P. micronema* Bleeker. It is a skin a little over a meter long; it must have been brought by M. Harmand or by M. Hahn."

The photographs referred to by Pavie show several large, freshly caught fish on a floating platform or the river bank. Pavie's giant catfish is not identifiable with *P. pleurotaenia*, *P. bocourti*, *P. micronema* or any other species named prior to *P. gigas* (Chevey 1930).

Food habits.—The food habits of juvenile and subadult *P. gigas* in the Mekong are not known. According to Pookaswan (1969), fishermen reported a greenish paste-like mass in the stomachs and intestinal tracts. Cannibalism among captive fry was reported by Pholprasith (1983:347). Captive *P. gigas* might grow more rapidly if supplied with their natural food.

Spawning grounds.—The story of spawning in Lake Tali evidently involves a misunderstanding. Smith (1945:373), overlooking or at least omitting the obviously fabulous or mythological part about the golden-scaled males, identified the Lac Tali in Pavie's account with Lake Tali or Erh Hai of Yunnan province, China. While *P. gigas* does occur in the mainstream of the Mekong River in southernmost Yunnan, it probably does not reach Lake Erh Hai. Although connected to the Mekong by the Yangpi River, the lake is at 2,140 m elevation and there are rapids or falls in the Yangpi which *P. gigas* presumably could not ascend (pers.

comm., X. L. Chu, 1985). The lake is inhabited by some 15 native fish species, including 12 Cyprinidae, two Cobitidae, and the symbranchid *Monopterus albus* (Chu 1980:80). In retrospect, it seems more likely that the "lac Tali" of Pavie's Laotians is the Grand Lac or Tonle Sap of Cambodia.

Location of the spawning grounds of *P. gigas* is poorly known, but two sites should be noted. First, the lower Mekong: Durand (1940) reported juveniles from Cambodia, including a specimen of 125 mm from Bac-Lieu, two specimens 150-185 mm from Kompong Cham, one specimen 285 mm from Chau Doc, one 420 mm from Peam Chikang, and one 450 mm from the Grand Lac, all caught in 1937-38. These are the smallest naturally occurring *P. gigas* ever reported. Bac-Lieu is in a mangrove area on the Cambodian coast about 50 km West of the mouth of the Bassac River (westernmost mouth of Mekong delta). Chau Doc is on the Bassac River about 180 km upstream from the South China Sea. Peam Chikang and Kompong Cham are on the mainstream Mekong, about 70 and 90 km upstream from Pnom Penh, respectively. This suggests spawning grounds in the Mekong delta or mouth, and perhaps in the adjacent brackish coastal waters at least as far West as Bac-Lieu. A spawning ground in the Tonle Sap is also possible. Second, a spawning ground has been identified in the mainstream of the Mekong River near Chieng Rai in northern Thailand. According to local fishermen, pla buk spawn in the Mekong near Ban Mueng Gan, 15 km upriver from Chiang Khong, Chiang Rai province (pers. comm. Snit Tongsanga, June 1989). Bhukaswan (1983:339) reported spawning at dawn 20 km upstream from Chiang Khong. Wang (or Ang) Pla Buk, on the Mekong in Ban Phatang, Amphur Srichiengmai, Nongkhai province and the mouth of the Mun River, both formerly noted for catches of *P. gigas* (Pookaswan 1969:5) are other possible sites of spawning activity although there seem to be no observations in support of this.

Growth rate.—Pangasius gigas undoubtedly has the most rapid growth rate of any species of *Pangasius*, and one of the most rapid of any freshwater fish species in the world. Artifically reared fry (Fig. 7) are 3.8 mm long at hatching, 8.45 mm by day two, 13.4 mm by day 7, and 28 mm by day 11 (pers. comm. A. Termvichakorn, Fisheries Department). In one study conducted by the Fisheries Department, fry averaging 13 cm and 17 grams grew to an average of 40 cm and 620 grams (a 400% increase in weight) in only four months. This helps explain why wild juveniles less than 500 mm long have been so rarely captured. Fry introduced into a large pond connected to the Chao Phraya near Samutprakan in 1985 grew to 100 kg by 1988

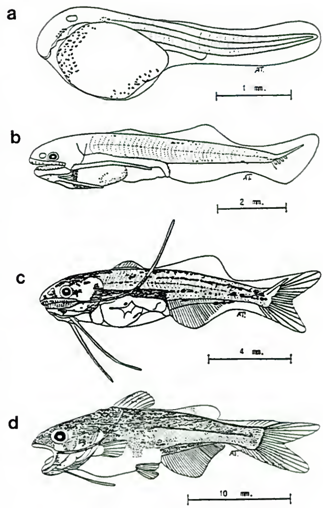

Fig. 7. *Pangasius gigas* larvae: a, newly hatched 3.8 mm SL; b, 2.5 days 8.4 mm; c, 7 days 13.4 mm; d, 11 days 28 mm (from stock artifically bred at Chieng Rai fisheries station). Drawn by Apichart Termvichakorn.

(pers. comm. W. Magtoon, June 1989). The growth rate in the Mekong River may be even faster, since the majority of *P. gigas* caught near Chieng Rai in 1988-89 weighing 150-200 kg or more presumably are individuals that were introduced into the Mekong near Chieng Rai as fry since 1984. Measurements of annuli in the fifth vertebral centra of a 230 cm, 135 kg *P. gigas* caught at Nongkhai in November 1967 indicated that it was six years old; and that it grew slowly in the first, faster in the second, and fastest in the third year, and therafter more slowly (Pookaswan 1969).

Adaptations for rapid growth in *Pangasius* and especially *P. gigas* should be looked for throughout the life cycle and at different levels of biological organization. For example, there presumably is a genetic difference between *P. gigas* and *P. hypophthalmus* which influences the difference in their growth rate and ultimate size. Other adaptations found in *P. gigas* which account for its rapid growth may be shared with other species of *Pangasius*. Among these are morphological and behavioral adapatations, including larval cannibalism, specialized larval dentition, gluttonous food habits, and highly distensible abdomen and alimentary canal.

The larval teeth of *P. gigas* have been noted by A. Termvichakorn and other Thai fisheries workers. These appear by day 2 and are retained until after day 7; by day 11 they have disappeared. Their presence perhaps corresponds with the period when the larvae are cannibalistic; however, the cannibalism and indeed the food habits of larval *P. gigas* have been observed only in captive conditions.

Fishery.—The giant Mekong catfish probably has been the object of traditional fisheries for many centuries. By 1950 the catch had declined from several hundred or more individuals per annum to a dozen or so, and fears began to be expressed that the species might become extinct (Serene 1951; Davidson 1975). Since 1984 the main fisheries has been at Chieng Khong in Chieng Rai province, Thailand. The fishing season begins in late March and lasts only one month. There has been a more or less steady increase in numbers caught, 15 in 1984 to 64 in 1990; the ratio of males to females caught is 2:1 (Tongsanga and Polprasit 1991). This difference possibly reflects differences in behavior rather than a true difference in the sex ratio; males tend to be caught earlier in the fishing season, and males and (and to a less extent females) tend to be caught together: on the same day or on consecutive days the catch tends to be all males or all females (Tongsanga and Polprasit 1991, fig. 3: 506).

Aquaculture.—In 1967 the Thai Fisheries Department launched a study of pla buk that eventually led to a breeding project. In May 1983 the first successful artifical breeding of wild adults caught in the Mekong River near Chiang Rai produced some 200,000 fry, but due to inadequate rearing techniques their survival was very poor. Successful breedings have been obtained every year since then except 1986. In 1984 five wild caught pairs were artifically bred, and 130,000 fry reared to 100-125 mm; some 80,000 were released into the Mekong, Chao Phraya, and other natural waters of Thailand. By 1986 some 8,000 had been distributed to fish farmers in 27 provinces; some 300,000 had been released in natural waters throughout the country. The Fisheries Department is continuing research to improve breeding techniques, increase survival of fry, and accelerate the growth rate in captivity. At this point it is uncertain whether the annual increase in fish caught at Chieng Khong since 1984 is due mainly to improved fishing methods or recruitment of introduced stock.

Common names.—According to Bhukaswan (1983:339), fishermen at Chiang Khong recognize three kinds of pla buk based on morphology, size, and color, called pla ma- fai, pla nang, and pla hua kum hang hum.

Distribution.—*Pangasius gigas* is endemic to the Mekong basin. Artificially reproduced fry have been introduced into the Chao Phraya and possibly other river systems in Thailand since 1985.

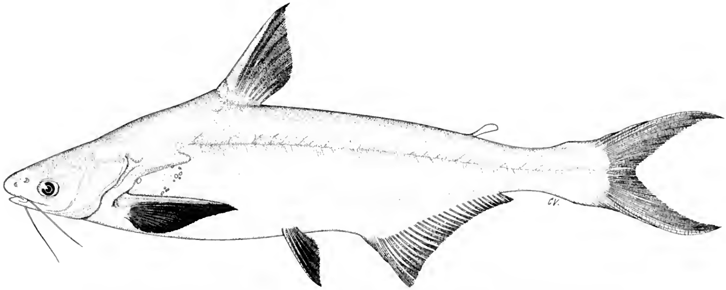

Fig. 8. *Pangasius humeralis*, 204 mm SL; Kapuas basin, Sintang (CAS 49408, paratype).

Pangasius humeralis Roberts
Figs. 2o, 8

Pangasius humeralis Roberts, 1989:131, figs. 100, 101c (type locality Sintang, Kapuas basin).

Material examined.—MZB 3680, 173 mm, Sintang market, T. R. Roberts, July 1976; (holotype); CAS 49408, 204 mm, Sintang market, T. R. Roberts, July 1976 (paratype); RMNH 28903, 2:312-389 mm, Sintang market, T. R. Roberts, July 1976 (paratypes).

Note on paratypes.—The original description of *P. humeralis* was based on the holotype and three paratypes. One paratype, 312 mm, was misplaced prior to publication and therefore was not listed. In November 1989 M. van Oijen and T. R. Roberts confirmed that the specimen had been sent inadvertently to RMNH along with the 389 mm paratype. Both specimens now bear catalog number RMNH 28903. The specimen illustrated in Roberts, 1989, fig. 100 is the 312 mm paratype, not the 389 mm paratype as indicated in the figure legend.

Comparative description.—*Pangasius humeralis* is distinguished from all other species of *Pangasius* except *P. nieuwenhuisii* by a greatly enlarged pectoral gland and very elongate humeral process extending fully two-thirds or three-quarters of distance to end of pectoral fin spine (versus half or less than half in all other species). Palatal teeth in a single large median patch, as in *P. kinabatanganensis*, *P. lithostoma*, and *P. nieuwenhuisii*. Eye small, diameter 29-35 in SL; gill rakers on first gill arch 19-22; anal fin rays 30-31; vertebrae 47-48. Pectoral fins jet black. Body without distinctive marks.

Pangasius humeralis is most similar to *P. nieuwenhusii*. Direct comparison of the 400 mm holotype of *P. niuwenhuisii* and 389 mm paratype of *P. humeralis* revealed that *P. nieuwenhuisii* has a much more pointed snout; angle subtended by snout tip and anterior border of eye much greater in *P. nieuwenhuisii*.

Size.—Attains about 40 cm standard length.

Distribution.—*Pangasius humeralis* is known only from the Kapuas basin of western Borneo.

Pangasius hypophthalmus Sauvage
Figs. 1f, 2e, 9

Helicophagus hypophthalmus Sauvage, 1878:235 (type locality Laos); Sauvage, 1881:170, pl. 7, fig. 1; Smith, 1945:370; Kottelat, 1984:881 (lectotype and paralectotype designation).

Pangasius hypophthalmus. Hora, 1923:166 (Bangkok); Fowler, 1934:88 (Bangkok); Hora, 1937:236.

Pangasius pleurotaenia Sauvage, 1878:235 (paralectotype only; Laos).

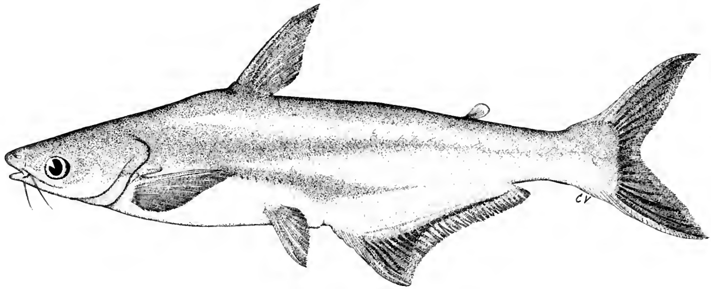

Fig. 9. *Pangasius hypophthalmus*, 216 mm SL; Chao Phraya basin, Pathumtani (NIFI 2254).

Pangasius sutchi Fowler, 1937:141 (type locality Bangkok).
?*Pangasius pangasius*. Hora, 1923:167 (identification only; Bangkok).
Pangasius pangasius. Smith, 1945:366 (Chao Phraya; Bangkok; Bung Borapet).

Material examined.—MNHN 745, 62 cm (mounted stuffed specimen with glass eyes, gill arches removed), Laos, Harmand (lectotype *P. hypophthalmus*); MNHN 744, 58 cm (mounted stuffed specimen with glass eyes, gill arches removed), Laos, Harmand (paralectotype *P. hypophthalmus*); MNHN A.6335, 2:249-2689 mm, Me-Nam [Chao Phraya], Harmand; ANSP 67902, 112 mm, Bangkok, R. M. de Schauensee, 1936 (holotype *P. sutchi*); ANSP 67903-905, 3: 105-127 mm, Bangkok, R. M. de Schauensee, 1936 (paratypes *P. sutchi*); MNHN A2389, 130 mm, Cambodge (paralectoype *P. pleurotaenia* designated by Kottelat, 1984:813); KUMF 1047, 160 mm, Rajburi, Meklong basin; KUMF 1045, 2:126-174 mm, Nakorn Sawan; CAS 67214, 2:150-155 mm, Nakorn Sawan market, T. R. Roberts, 10-12 April 1989; CAS 67369, 160 mm, Suphanburi market, T. R. Roberts NIFI 2254-56, 3:216-236 mm, Pathumtani, Chao Phraya basin; NIFI 2269, 2:168-175 mm, Khong Chiam, Ubol prov., Mekong basin; CAS 67215, 129 mm, Ubol Ratchatani market, T. R. Roberts, 24-25 Dec. 1989; NRM BJO/ 1935.111.5271, 275 mm.

Lectotype and paralectotypes of P. hypophthalmus.—All three (of the originally three or four) extant syntypes of *P. hypophthalmus* have terminal mouths and 8 or 9 rays in both pelvic fins. Thus they belong to the subgenus *Pangasianodon* comprising the two species until now recognized as *P. gigas* and *P. sutchi*. The two smaller syntypes have well developed maxillary and mandibular barbels and well developed gnathal and palatal tooth bands and are therefore identifiable with *P. sutchi*, since in *P. gigas* of comparable sizes these features are missing or vestigial. Unfortunately, the gill arches of the three specimens were removed when they were dried and mounted, thus the diagnostic evidence from the gill rakers is unavailable. In the large (87 cm) syntype the mental barbels and oral toothbands are entirely absent, as in *P. gigas* larger than 30-50 cm.

The original description of *P. hypophthalmus*, is based on the smaller syntypes only. The large syntype was not mentioned until the redescription of the species by Sauvage (1881). Examination of the specimens and a careful reading of the text indicates that the original description may have been based only on the 62 cm specimen designated as lectotype by Kottelat (1984:881). This specimen has oral dentition only partially intact (most of the teeth evidently having been scraped off during preparation) and the anal fin damaged, so that its rays are

unusually short. The damage is identical or similar to that inflicted by the fin-eating tetraodontid *Chonerhinos nefastus* Roberts on *Pangasius* caught in gill-nets (see Roberts 1982, fig. 9). This is the specimen figured in Sauvage (1881, pl. 7, fig. 1).

Comparative description.—*Pangasius hypophthalmus* differs from all other species of *Pangasius* in having small gill rakers regularly interspersed with larger ones on the gill arches. It differs from all other species except *P. gigas* in having 8 (occasionally 9) pelvic fin rays instead of only 6, and a terminal mouth, with tooth band of upper jaw entirely covered by lower jaw when mouth is closed. From *P. gigas* it differs in having well developed instead of rudimentary gill rakers, relatively longer barbels, narrower head, and maximum length about 90 cm instead of 3 m or more.

Juveniles typically have well defined midlateral and abdominal stripes separated at level of pectoral fin origin; abdominal stripe although fainter posteriorly, sometimes extending to above end of anal fin; middle of anal fin with a faint dark stripe not seen in other species of *Pangasius*; caudal lobes striped, but stripes broader and less well defined than in *P. larnaudii* and *P. pleurotaenia*; dark color of upper and lower caudal lobe stripes continuous with dark color on base of short rays in middle of caudal fin. Larger specimens are less distinctively colored.

Gill rakers.—The peculiar gill rakers of *P. hypophthalmus* were first noted by Durand (1949:116) who stated "there are always well developed gill rakers, of lanceolate form, between which are sometimes very small or rudimentary gill rakers. Depending on whether these are counted, one finds in a given example 15 or 40 gill rakers on lower limb of the first arch."

Swimbladder.—Browman and Kramer (1985) reported that *P. hypophthalmus* is a continuous, obligate air breather, and identified the swimbladder as the most likely accessory breathing organ, since it is "large, trabeculated, well vascularized, and the only obvious gas-containing structure in the body" (p. 997). Our observations lead us to doubt such a role for the swimbladder. In fresh specimens we examined, the swim bladder and particularly the trabeculae do not seem well vascularized. The swimbladder, although large, is relatively rigid, due largely to the trabeculae, which apparently function as struts or tresses. We would expect an accessory breathing organ to be distensible as well as more richly blood supplied, and suggest that if *P. hypophthalmus* and perhaps other species of *Pangasius* are air-breathers, the accessory breathing organ is more likely the stomach or alimentary canal. It should be noted that a large, trabeculated swim bladder is characteristic of all species of *Pangasius*, not just *P. hypophthalmus*. We further suggest that gulping water and air at the surface may in itself be adaptive respiratory behavior, even without an accessory breathing organ.

Size.—*Pangasius hypopthalmus* seldom is caught in the wild any more. The usual maximum size of fish reared in ponds is 6-7 kg and 80 cm SL. At Nongekai market in April 1990 the first author observed a fish of 15.5 kg and 1.3 m SL, evidently caught in the Mekong. It had eight pelvic fin rays and accessory gill rakers characteristic of the species, but differed from all other *P. hypophthalmus* observed in having upper jaw projecting noticeably beyond lower (rather than jaws equal).

Distribution.—The natural range of *Pangasius hypophthalmus* includes the Mekong, Chao Phraya, and perhaps Meklong basins (Thailand, Laos, Kampuchea, and Vietnam). Introduced into additional river basins for aquaculture.

Pangasius kinabatanganensis new species
Figs. 2p, 10

Pangasius nieuwenhuisi. Inger and Chin, 1962:148, fig. 75 (Kinabatangan).
Pangasius sp. undet. Roberts, 1989:131, fig. 101d (dentition).

Holotype.—FMNH 68042, 238 mm, Kinabatangan R. at Deramakot, R. F. Inger, May 1956.

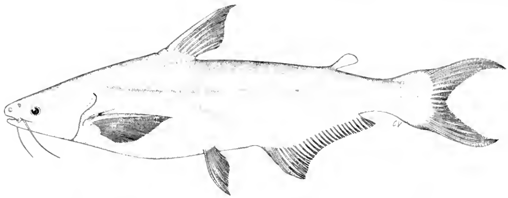

Fig. 10. *Pangasius kinabatanganensis*, 217 mm SL; Kinabatangan basin (FMNH 68041, paratype.

Paratypes.—FMNH 68041, 217 mm, Kinabatangan R. at Deramakot, R. F. Inger, May 1956; FMNH 68043, 590 mm (head and fins only), Kinabatangan R. at Deramakot, R. F. Inger, May 1956; FMNH 44855, 2:129-136 mm, Kinabatangan R. at Malapi, J. A. Tubb, June 1949.

Comparative description.—*Pangasius kinabatanganensis* differs from all other other species of *Pangasius* except *P. lithostoma* in having the combination of palatal dentition consisting of a single large median (entirely vomerine?) toothplate and a humeral spine extending posteriorly one-half or less the distance to end of adpressed pectoral fin spine. It differs from *P. lithostoma* in having only 27-30 anal fin rays (instead of 40-41). Gill rakers on first gill arch 7-9+15-17=22-25. Vertebrae 49-50.

Although it has fewer rays, the anal fin of *P. kinabatanganensis* is much larger than that of *P. lithostoma*; the anterior anal fin rays are one and a half times as long as in *P. lithostoma*, the posterior rays fully twice as long. The adipose and pelvic fins are also much larger in *P. kinabatanganesis*. In the 590 mm paratype the palatal tooth plate is enormous, but even so it does not project so strongly downwards from the roof of the mouth as does the toothplate in *P. lithostoma*. In the smaller holotype and other paratypes of *P. kinabatanganesis* the toothplate is much smaller and relatively flat rather than strongly convex.

Size.—Attains at least 60 cm standard length.

Etymology.--Named for the Kinabatangan basin (see below).

Distribution.—*Pangasius kinabatanganensis* is known only from the Kinabatangan basin, northeastern Borneo.

Pangasius krempfi Fang and Chaux
Figs. 1g, 2g, 11

Pangasius micronema. Tirant, 1883:16 (rivière de Hue).

?*Pangasius pangasius*. Chevey, 1932:37, pl. 11.

Pangasius krempfi Fang and Chaux *in* Chaux and Fang, 1949:343, fig. 5 (type locality "en mer á Bong Lao").

Sinopangasius semicultratus Chang and Wu, 1965:11 (type locality South China Sea off Paihai and Shanwei, Kwangtung province).

Material examined.—MNHN 1966-729, 334 mm, Bong Lao (holotype *P. krempfi*); MGHNL 3261, 2:281-302 mm, rivière de Hue, Annam, Tirant, 1882 (previously identified as *P. micronema*); FMNH 71996, 3: 242-265 mm, Vietnam, Haiphong and Hanoi, A. Owston, July 1911; NIFI 2237, 538 mm, Nongkhai market; NIFI 2238, 600 mm Bungkan market, Nongkhai province; NIFI 2289, 530 mm, Phonpisei, Nongkhai province.

Diagnosis.—*Pangasius krempfi* is characterized by a broadly rounded, elongate snout, subterminal mouth, palatal teeth in two palatal and two vomerine bands, swim bladder with three chambers extending to or beyond end of anal fin base, 19-22 gill rakers on first gill arch, body and fins without distinctive marks, males with short filaments on dorsal and pelvic fins, anal fin rays 31-34, vertebrae 52. Dorsal surface of head and body iridescent greenish-blue (slate gray after death), ventral surfaces milk white. Fins colorless. No distinctive markings on body or fins.

Reproduction.—No individuals under 225 mm SL have been observed, and it is unknown

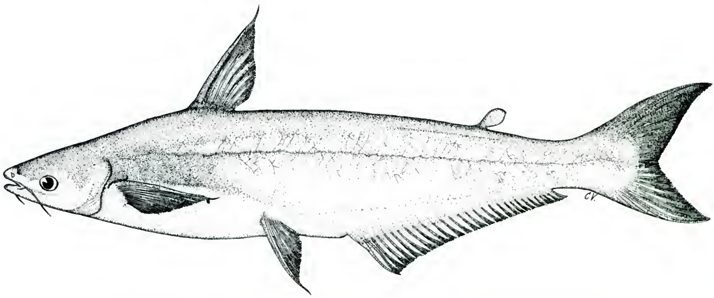

Fig. 11. *Pangasius krempfi*, 538 mm SL; Mekong basin, Nongkhai (NIFI 2237).

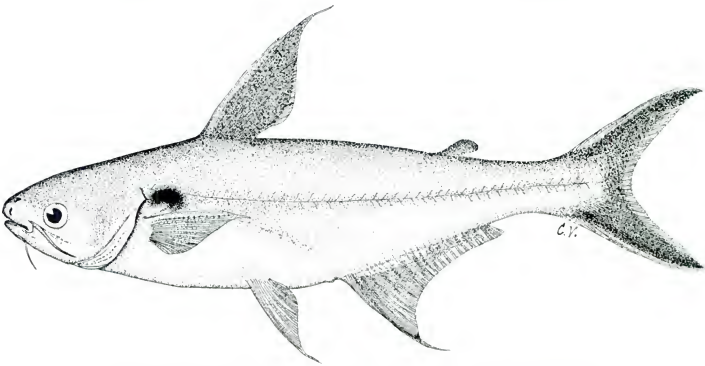

Fig. 12. *Pangasius larnaudii*, 206 mm SL; Mekong basin, Nongkhai (NIFI 2273).

where spawning occurs. At Khong Chiam on the Mekong River in Jan.-April 1990 the first author observed some 30 freshly caught fish of 60-80 cm SL, many with maturing ovaries and testes. These fish evidently were migrating, but whether upstream or downstream is unknown.

Distribution.—Pangasius krempfi is known from South China Sea off Paihai and Shanwei, Kwantung; South China Sea at Bong Lao [we have been unable to find Bong Lao in standard gazetteers and atlases of Southeast Asia]; rivière Hué, Annam, east coast of Vietnam; and from Mekong River in Nongkhai and Ubol provinces, Thailand (numerous individuals 60-80 cm observed at Khong Chiam by first author Jan.-April 1990).

Pangasius larnaudii Bocourt
Figs. 1f, 2d, 12

Pangasius larnaudii Bocourt, 1866:15, pl. 1, fig. 2 (type locality Ajuthia); Smith, 1945:359, fig. 81.
Pangasius taeniura Fowler, 1935:98, fig. 19 (type locality Bangkok).
Pangasius burgini Fowler, 1937:141, figs. 24-26 (type locality Bangkok).
Pangasius taeniurus. Smith, 1945:367.

Material examined.—MNHN 1549, 270 mm, Ajuthia, F. Bocourt (syntype *P. larnaudii*); ANSP 61753-54, 2:66.2 mm, Bangkok, de Schauensee (holotype and paratype *P. taeniura*); ANSP 67901, 188 mm, Bangkok, de Schauensee (holotype *P. burgini*); NIFI 450, 270 mm, Nan R., Chao Phraya basin; NIFI 2268, 141 mm, Saraburi, Chao Phraya basin; KUMF 1036, 149 mm, Lopburi, Chao Phraya basin; NIFI 436, 2: 81.8-96.0 mm, Ayuthya; CAS 67202, 192 mm, Ayutthaya market, T. R. Roberts, 5-7 April 1989; KUMF 1037, 68-70 mm, Suphanburi, Chao Phraya basin; NIFI 2273, 206 mm, Nongkhai; NIFI 2271, Mukdaharn, Mekong basin; CAS 67203, 241 mm, Khong Chiam market, T. R. Roberts, May 1989; NIFI 2267, 107-180 mm, Ubol, Mekong basin; CAS 67201, 2:50.8-91.3 mm, Ubol Ratchatani market, T. R. Roberts, 28 June 1985.

Notes on synonymy.—*Pangasius burgini* was placed as a junior synonym of *P. larnaudii* by Smith (1945:359, 361), and we concur. The holotype has 14 gill rakers on first arch, 32 anal fin rays, filamentous extensions on dorsal and pelvic fins, and the diagnostic black humeral spot of *P. larnaudii*.

Pangasius taeniura was recognized by Smith (1945:367) but no additional specimens have been identified since the original description. Although the humeral spot is not evident in the two small type specimens, they do have well developed stripes on both caudal fin lobes, 13 gill rakers on first gill arch, 30-31 anal fin rays, and about 45 vertebrae, all in agreement with *P. larnaudii*; we are unable to identify them with any other species.

Comparative description.—*Pangasius larnaudii* differs from all other species of *Pangasius* in having a large, black humeral spot. Dorsal, pectoral, pelvic, and anal fins with filamentous extensions. Upper and lower caudal fin lobes usually bearing well defined dark stripes. Gill rakers on first gill arch 12-16, anal fin rays 28-32, total vertebrae 43-46.

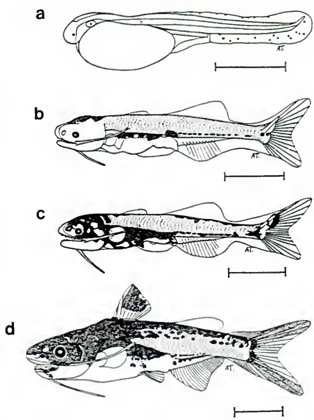

Fig. 13. *Pangasius larnaudii* larvae: a, 12 hrs 3.5 mm SL; b, 4 days 8.4 mm; c, 8 days 8.8 mm; d, 18 days 23 mm (from stock artifically bred at Nongkhai fisheries station). Drawn by Apichart Termvichakorn.

Fry.— Artifically reared fry (Fig. 13) are 3.5 mm at 12 hrs, 8.4 mm at 4 days, 8.8 mm at 8 days, and 23 mm at 18 days. Distinctive larval teeth present in 12 hr and 4 day larvae.

Remarks.—According to Bocourt (1866:16-17), a century ago *P. larnaudii* "was not sold in the markets of Bangkok because it was too expensive; also, it was reserved for consumption by important people." He also reported that "its flesh is extremely delicate and succulent; it is raised and fattened at Ayuttaya, in watercourses closed off by bamboo grill." The species is not utilized currently in aquaculture.

Size.—Attains about 80 cm standard length.

Distribution.—*Pangasius larnaudii* occurs in the Mekong and Chao Phraya basins.

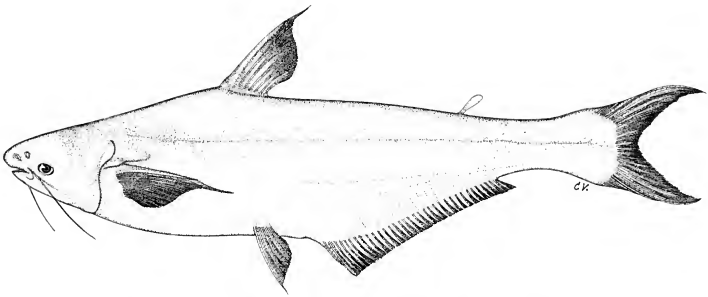

Fig. 14. *Pangasius lithostoma*, 270 mm SL; Kapuas basin, Sintang (IBRP 6861).

Pangasius lithostoma Roberts
Figs. 1i, 2q, 14

Pangasius lithostoma Roberts, 1989:132, fig. 102 (type locality, Sintang, Kapuas basin, western Borneo).

Material examined.—MZB 3678, 196 mm, Sintang market, T. R. Roberts, July 1976 (holotype); CAS 49406, RMNH 28901, USNM 230299, 3:181-214 mm, Sintang market, T. R. Roberts, July 1976 (paratypes).

Comparative description.—Pangasius lithostoma is distinguished from all other species of *Pangasius* in having palatal dentition consisting of a single greatly expanded, convex toothplate projecting strongly downward from roof of mouth. It further differs from *P. kinabatanganensis* in having 40-41 anal fin rays (instead of 27-30), and from *P. humeralis* and *P. nieuwenhuisii* in having humeral gland only moderately enlarged and humeral process less than half rather than more than two-thirds as long as pectoral spine. Gill rakers on first gill arch 22-26. Vertebrae 21+31=52 (in three specimens). Fins dusky, body without distinctive marks.

Size.—Largest specimen examined 214 mm standard length, probably grows much bigger.

Distribution.—Pangasius lithostoma is known only from the Kapuas basin of western Borneo.

Pangasius macronema Bleeker
Figs. 1o, 2a, 15

Pangasius macronema Bleeker, 1851a:11 (type locality "Banjermassing, in fluviis"). Bleeker, 1862b:74, pl. 75, fig. 3.

?*Pangasius delicatissimus* Bleeker, 1862b:73 (type locality Krawang, Java; short description based on unpublished drawing; *nomen dubium*, unavailable for zoological nomenclature; See Weber and de Beaufort, 1913:262).

Pangasius siamensis Steindachner, 1879:393 (type locality "Menam-Fluss bei Bangkok").

?*Pangasius aequilabialis* Fowler, 1937:140, figs. 20-23 (type locality Bangkok).

Material examined.—RMNH 6855, 10:70.5-124 mm, Borneo, Bleeker collection (no other data); BMNH 1863.12.4.66, 147 mm, Bleeker collection, no other data; NMW 76998, 198 mm (syntype *P. siamensis*); NMW 45469, 198 mm (syntype *P. siamensis*); ANSP 67897, 110.5 mm, Bangkok, R. M. de Schauensee (holotype); ANSP 67898-90, 2:90.4-91.9 mm (paratypes *P. aequilabialis*); NIFI 2242, 6:72-110 mm, Nan R., Chao Phraya basin; ANSP 88041, 119 mm, MePoon, R. M. de Schauensee, 1936; NIFI 448, 3:62.0-108 mm,

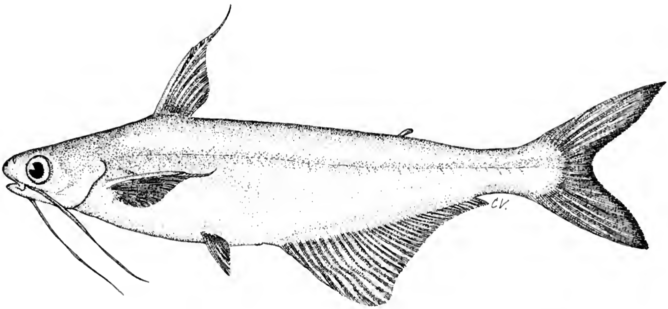

Fig. 15. *Pangasius macronema*, 185 mm SL, male; Mekong basin, Nongkhai (NIFI 2247).

Nakorn Sawan; NIFI 445, 136 mm, Nakorn Sawan; NIFI 479, 160 mm, Nakorn Sawan; CAS 67206, 151 mm, Nakorn Sawan market, T. R. Roberts, 4-5 Feb. 1989; NIFI 444, 6:63.0-135 mm, Ayuthya; ZSM/CMK 4872, 2:96.7-96.8 mm, Ayuttaya market, M. Kottelat, 4-5 March 1985; CAS 67204, 3:149-174 mm, Ayutthaya market, T. R. Roberts, 5-7 April 1989; NIFI 2244, 2:103-104 mm, Tachin R., Suphanburi, Chao Phraya basin; KUMF 1053, 2:80-98 mm, Nontaburi, Chao Phraya basin; ANSP 60640-41, 2:66.3-98.0 mm, Bangkok, R. M. de Schauensee, May 1934; ANSP 87432, 16:73.5-130 mm, Bangkok, R. M. de Schauensee, 1936; CAS 67205, 30:103-143 mm, Bangkok market, T. R. Roberts, March 1989; KUMF 1054, 2:78-95 mm, Pasak R., Chao Phraya basin; CAS 67207, 6:123-142 mm, Bangpakong R. near Prachinburi, T. R. Roberts, 22 March 1989; NIFI 2247, 4:44.9-185 mm, Nongkhai, Mekong basin; CAS 67208, 128 mm, Mekong R. at Bung Kla, T. R. Roberts, 7 July 1985; NIFI 2293, 7:36.0-52.3 mm, Nakorn Phanom, Mekong basin; NIFI 446, 132 mm, Kemarat, Mekong basin; NIFI 2288, 50.0 mm, Ubol, Mekong basin; ANSP 77239, 125 mm, Saigon, H. Rutherford, Dec. 1934; MGHNL 3258, 3:166-179 mm, rivière Hué, Annam, Tirant, 1882; ZMA 115.738, 11:113-167 mm, Bandjermasin, H. A. Lorentz, 13 May 1909.

Notes on synonymy.—Despite a considerable distributional gap, our samples from Indonesia and Indo-China appear to represent a single species, and therefore we relegate *P. siamensis* as a junior synonym of *P. macronema*. The types of *P. aequilabialis* appear similar to *P. macronema* in all respects except in having the lower jaw extending to snout tip rather than subterminal; re-evaluation of the status of this nominal species should be undertaken when additional specimens become available.

Comparative description.—*Pangasius macronema* is a relatively small, slender species differing from all other *Pangasius* by its relatively narrow head and mouth, and numerous very slender or elongate gill rakers (37-45 on first gill arch). Mandibular and maxillary barbels typically reaching posteriorly to or beyond pectoral fin origin. Abdomen short, abdominal vertebrae only 14-16 (16 or more in all other species).

Eyes large, diameter 5.2-9.6% SL. Mouth narrow, angle of lower jaws less than 90 degrees. Adipose fin small, width 0.9-1.2% SL. Midlateral and abdominal stripes well defined, separate at level of pectoral fin origin.

Sexual dimorphism and scratches.—We have observed numerous samples of *P. macronema* from the Mekong and Chao Phraya basins in which males have the anal fin greatly enlarged, with anal fin rays much longer than in females. In large fresh samples with gravid females

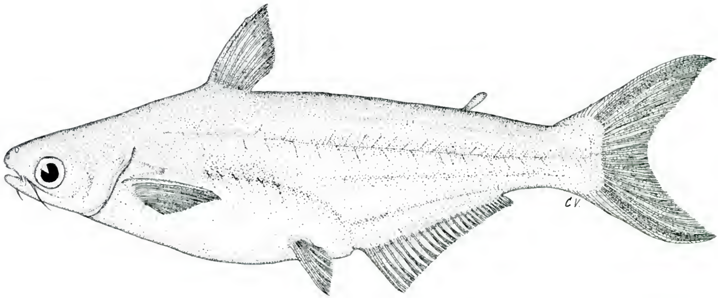

Fig. 16. *Pangasius micronema*, 128 mm SL; Mekong basin, Kemarat (NIFI 442).

observed at Ayutthaya and Singburi in March-April 1989, virtually all males but none of the females had a long, straight, bleeding scratch, presumably inflicted by the female's pectoral spine while engaged in the spawning embrace. The scratches, observed on several hundred males, are usually present on both sides of the body and are remarkably constant in position and length. There is usually only one fresh scratch on each side; it extends from a point slightly posterior to a vertical through origin of anal fin to above end of anal fin base, and lies in the superficial groove or furrow formed at the meeting of the hypaxial lateralis and anal fin pterygial musculature. Depending on the male's length, the scratches are about 40-60 mm long. Comparable scratches have not been observed in any other species. Based on our limited samples, *P. macronema* from Indonesian localities apparently has similar sexual dimorphism of the anal fin, although less pronounced than in the more extreme samples observed from Thailand. Sexual dimorphism of the anal fin has not been observed in any other species of *Pangasius*.

Size.—Maximum size about 20 cm standard length.

Distribution.—Pangasius macronema has a disjunct distribution. In mainland Asia it occurs only in the Mekong and Chao Phraya basins. In the Malaysian or Indonesian archipelago, it is known only from Java and southern Borneo.

Pangasius micronema Bleeker
Figs. 1j, 2b, 16

Pangasius micronema Bleeker, 1847:8 (type locality Java); Bleeker, 1862b:75, pl. 87, fig. 2.
Pangasius rios Bleeker, 1851b:205 (type locality "Bandjermassing, in fluviis") Bleeker, 1862b:74, pl. 79, fig. 2.
Pseudolais tetranema Vaillant, 1902:52, fig. 3 (type locality "Tepoe, bords du Mahakam", eastern Borneo).
Pangasius dezwaani Weber and de Beaufort, 1912:14 (type locality Taluk, Sumatra).
?*Pangasius dezwaani*. Chevey, 1932:39, pl. 12.
?*Pangasius hoeksi* Hardenberg, 1948:370 (type locality Kapuas River).
Pangasius tubbi Inger and Chin, 1959:287 (type locality Kinabatangan River, northeastern Borneo).

Material examined.—RMNH 6856, 3:145-440 mm, Bleeker collection, no other data; BMNH 1863.12.4.92, about 106 mm, Bleeker collection (apparently the only extant Bleeker specimen of *P. rios*; in very poor condition, tail missing); BMNH 1863.12.4.82, 251 mm, Bleeker collection, Java (in poor condition, flacid and bleached; the only Bleeker

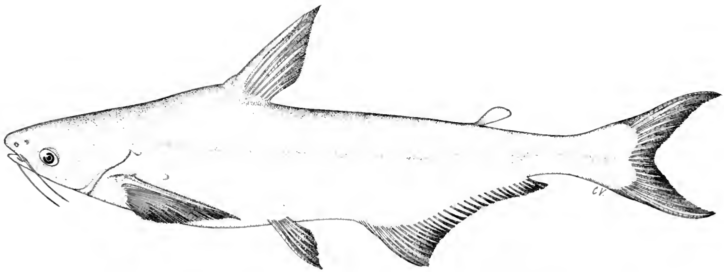

Fig. 17. *Pangasius myanmar*, 230 mm SL; Rangoon, Myanmar (CAS-SU 33787, holotype).

specimen with locality data from Java); ZMA 115.736, 175 mm, Kediri, Java; ZMA 113.011, 345 mm, Taluk [upper Indragiri], Sumatra (holotype *P. dezwaani*); ZMA 115.735, 8:80.1-158 mm, Djambi, Batang Hari, P. H. Moolenburgh, 22 Dec. 1909; ZSM/CMK 4739, 3:170-212 mm, Jambi market, M. Kottelat, 9 Dec. 1984; ROM 53696, 2:273-292 mm, Akah R., Baram basin, M. H. Ang, 16 March 1981; ROM 53698, 231 mm, Sungai Tinjar, Baram basin, M. H. Ang, 28 April 1981; MNHN 1891/463-465, 3:107-231 mm, Borneo, Kapuas, Chaper, 1890; FMNH 68047, 225 mm, Kinabatangan R. near Deramakot, northeastern Borneo, R. F. Inger, May 1956 (holotype *P. tubbi*); FMNH 68044-46, 68048, 6:63.7-120 mm, Kinabatangan R. near Deramakot, R. F. Inger, April-May 1956 (paratypes *P. tubbi*); FMNH 44859, 2:81.3-85.6 mm, Kinabatangan R. near Lamag, Fisheries Dept., 20 Jan. 1949 (paratypes *P. tubbi*); FMNH 44856-57, 3:134-150 mm, Kinabatangan R. near Lamag, G. Keith, 30 July 1949 (paratypes *P. tubbi*); FMNH 44858, 215 mm, Kinabatangan R. at Melapi camp, J. A. Tubb, 23 June 1945 (paratype *P. tubbi*); FMNH 44860, 6:89.8-149 mm, Segama R., northeastern Borneo, P. K. Chin, 26 May 1950 (paratypes *P. tubbi*); RMNH 7545, 2:246-259 mm, Bo, Mahakam; ZMA 115.743, 181 mm, Bandjermasin, H. A. Lorentz, 13 May 1909; CAS-SU 31032, 172 mm, Bukit Merah, Perak, Malaya, W. Birtwistle, 1934 or earlier; CAS-SU 31031, Chandra Dam, Perak R., A. W. Herre, March 1934; CAS-SU 14255, 32725, 34930, 6:118-271 mm, Perak R. Chanderoh Dam, A. W. Herre, March-April 1937; MNHN 1988-1171, 148 mm, Cambodge, no other data; NIFI 442, 128 mm, Kemarat; NIFI 2239, 430 mm, Nongkhai; NIFI 2290, 2:90.0-97.7 mm, Bungkan, Nongkhai prov.; KUMF 1041, 124 mm, Bangkok.

Notes on type specimens and synonymy.—The holotype of *P. dezwaani* has head length 5.3 times in SL; palatal teeth in two palatine and two vomerine patches; gill rakers on first gill arch 4+11=15; anal fin rays 34.

Pangasius tubbi, based on specimens from physiographically isolated Kinabatangan basin of northeastern Borneo, has relatively long barbels, small eyes, and slightly high vertebral counts: 46(1), 47(3), and 48(3) (versus 44-46 in *P. micronema* from all other localities). Specimens of *P. micronema* with relatively large eyes and low vertebral counts occur in the Malay peninsula (nearly all from Chanderoh Dam) and Sarawak. However, specimens with relatively small eyes and low vertebral counts (44) are also known, from Cambodge and Java. We regard these differences as intraspecific variation, and note that eye size in particular is likely to be influenced by environmental factors.

Diagnosis.—*Pangasius micronema* is characterized by very thin, short barbels; maxillary barbel usually reaching but slightly posterior to eye and length of mandibular barbel less than eye diameter; dorsal and pectoral spines very slender; some specimens with eye relatively larger than in any other species of *Pangasius.*

Gill rakers usually 13-20; 24 in one specimen from Java. Anal fin rays 29-38. Total vertebrae 44-48.

Size.—Maximum size to about 60 cm standard length.

Distribution.—*Pangasius micronema* occurs in the Mekong basin, rivière Hue in Annam, Malay peninsula, and Indonesia, including Sumatra, Java and Borneo. It is particularly widely distributed in Borneo, where it inhabits most of the major river basins, including the Kapuas, Mahakam, Rejang, and Kinabatangan.

Pangasius myanmar new species
Figs. 2k, 17

Holotype.—CAS-SU 33787, 230 mm, Rangoon, A. W. Herre, April 1937.

Paratype.—NRM MAL/1934.4040, 107 mm, Rangoon, R. Malaise, 30 Nov. 1934.

Comparative description.—*Pangasius myanmar* is similar to *P. pangasius* but differs from it by having a narrower and more transverse mouth (width of gape 11.9-14.5 vs. 8.3-10.4 in *P. pangasius*; shorter barbels; palatal dentition with short oval palatine patches and a median oval vomerine patch (instead of relatively elongate palatine bands and two vomerine bands); fewer gill rakers (20-21 vs. 23-28, see Table 2); posterior swim bladder chamber cylindrical, posteriorly rounded (vs. tapered, posteriorly pointed), and more vertebrae (46-47 vs. 42-45, see Table 3). It is also similar to *P. conchophilus*, but differs from that species in having vomerine toothplate only half as wide, more vertebrae (Table 1), higher modal count of gill rakers (Table 2), and 32 instead of 25-30 anal fin rays.

Although only two specimens of this new species are available, they are readily distinguished from *P. pangasius* from Rangoon and other localities. The larger specimen (230 mm holotype) initially was recognized as distinct from *P. pangasius* due to its distinctive palatal dentition, which is quite different from that of any *P. pangasius* observed (compare Figs. 2c and 2k). The smaller specimen (107 mm paratype), originally part of a lot with four specimens of *P. pangasius* in an identical state of preservation, was first recognized as the new species due to its narrow head and mouth. The identity of the paratype with the holotype was confirmed by its counts of gill rakers (21) and vertebrae (46). Although the paratype has the vomerine teeth in two oval patches clearly separate at the midline, this is to be expected in smaller specimens; the palatine teeth bands are oval and shorter than the vomerine tooth bands, resembling the condition in the holotype. The four specimens of *P. pangasius* originally from the same lot have palatine teeth in elongate bands up to twice as long as the vomerine tooth patches. The maxillary barbel fails to reach the pectoral spine origin in the 230 mm holotype, whereas in a 261 mm specimen of *P. pangasius* from Rangoon it reaches well beyond pectoral spine origin. In the 107 mm paratype the maxillary barbel extends to the pectoral spine origin, but in four specimens of *P. pangasius* from the same sample it reaches to the anterior third of pectoral spine.

The holotype has swim bladder with two chambers confined to abdomen; posterior chamber cylindrical and posteriorly rounded (not tapered). A 261 mm *P. pangasius* from Rangoon has posterior chamber tapered and extending beyond abdomen to above anterior third of anal fin. In 107 mm paratype posterior chamber of swim bladder also cylindrical and posteriorly rounded; four *P. pangasius* obtained with it have posterior chamber confined to abdomen but tapered, posteriorly pointed.

The following proportional measurements are from the holotype (expressed as times in standard length): head (to upper angle of gill opening) 4.8; snout 24.0; eye (horizontal diameter of orbit) 8.7; interorbital width 8.5; internarial width 19.5; maxillary barbel 7.7; mandibular barbel 9.5; mouth width (inner transverse measure at rictus) 47.9; premaxillary toothplate transverse width 14.8; palatal toothplate transverse width 17.8; body width (at outside of humeral processes) 5.8; body height (at dorsal fin origin) 4.6; predorsal length 2.8; preanal length 1.7; caudal peduncle length

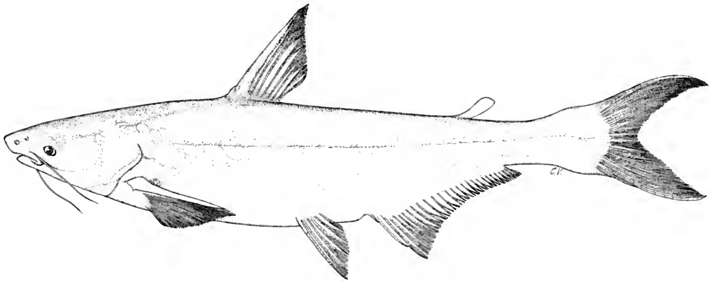

Fig. 18. *Pangasius nasutus*, 225 mm SL; Kapuas basin, Sintang (IBRP 7244).

6.5; caudal peduncle depth 15.0; dorsal fin spine 5.8; pectoral fin spine 4.9; humeral process (from pectoral spine origin) 9.9; pelvic fin 8.9; longest anal fin ray 9.3; anal fin base 3.6; adipose fin length 15.2; adipose fin base 54.8; anterior swim bladder chamber 8.0; posterior swim bladder chamber 6.5.

Etymology.—Named for the country of Myanmar (see below).

Distribution.—*Pangasius myanmar* is known only from Rangoon, Myanmar (formerly Burma).

Pangasius nasutus (Bleeker)

Figs. 1k, 21, 18

Pseudopangasius nasutus Bleeker, 1862c:72 (type locality "Bandjermassin, in fluviis"); Bleeker, 1862b:76, pl. 77, fig. 1.

Pangasius nasutus. Günther, 1864:63.

Pangasius ponderosus Herre and Myers, 1937:67, pl. 6 (type locality Chandra Dam, Perak, Malaya); Hora and Gupta, 1941:38 (Kuala Tahan, Pahang).

?*Pangasius macronema*. Inger and Chin, 1962:146-148 (Labuk, northeastern Borneo).

Material examined.—BMNH 1863.12.4.113, 210 mm, Bleeker collection (apparently the only Bleeker specimen and presumably holotype of *P. nasutus*); CAS-SU 14162, 558 mm, Chandra Dam, Perak, A. W. Herre, March 1934 (holotype *P. ponderosus*); UMMZ 155721, 270 mm, Palembang; ZMA 115.739, 460 mm, Djambi, Batang Hari, Moolenburgh, Jan. 1910; BMNH 1982.3.29.177, CAS 49407, MZB 3679, RMNH 28902, UMMZ 209855, and USNM 230300, 7:148-215 mm, Sintang market, Kapuas River, T. R. Roberts, July 1976; FMNH 44854, 70.5 mm, Labuk R., northeastern Borneo, A. Jones, July 1950.

Diagnosis.—*Pangasius nasutus* is distinguished from all other species of *Pangasius* by having an inferior mouth, with snout strongly projecting and tooth band of upper jaw entirely exposed when jaws are closed. In juveniles the snout is very pointed, perhaps more than in any other species, and this trait apparently is retained in larger subadults than in any other species, but in large adults the snout becomes rounded. In juveniles and subadults the jaw teeth are very sharp and project perhaps more strongly than in any other species, but this characteristic also is not noticeable in large adults. Dorsal and pectoral spines long, stouter than in any other species of *Pangasius*. In two Kapuas specimens 148-170 mm eye diameter 42-49 times in SL, much smaller than in specimens of comparable size of any other *Pangasius*. Body and fins without distinctive marks. Gill rakers on first gill arch 17-21. Anal fin rays 27-30. Vertebrae 43-45.

Remarks.—Our two largest specimens, 460

mm Batang Hari and 558 mm Perak (holotype *P. ponderosus*), have been compared side by side; they are so similar in all respects that we have no doubt as to their conspecificity. Specifically, they appear virtually identical in relative eye size (exposed portion of eye respectively 52 and 48 times in SL), barbel length (although the barbels of *P. ponderosus* holotype are all bitten off near the tip), rounded but strongly projecting snouts, and inferior mouth, and strong dorsal and pectoral fin spines. They differ from the smaller specimens of *P. nasutus* examined only in having the snout rounded rather than strongly pointed, and the jaw teeth less strongly projecting. Since the pointed condition of the snout is known to change to rounded or truncate with growth in *P. conchophilus* and *P. pangasius*, we think it also changes in *P. nasutus*, and predict that juvenile *P. nasutus* with sharply pointed snouts will be found in Perak and Pahang.

The 70.5 mm specimen from Labuk, previously identified as *P. macronema*, is clearly not that species. We tentatively identify it as *P. nasutus*. Its standard length is less than half that of the next smallest specimen of *P. nasutus* examined by us, and its locality far removed from other localities of *P. nasutus*. The specimen has 8+13 gill rakers on first gill arch, rugose supraoccipital and other cranial bones, very large adipose fin, 31 anal fin rays, and 17+27=44 vertebrae. Snout strongly pointed. Tooth band of upper jaw entirely exposed when mouth is closed. Palatal teeth in four slender discrete patches; mediad patches widely separated from each other (all other specimens of *P. nasutus* examined with a large mediad vomerine tooth patch and smaller lateral palatine tooth bands).

Food habits.—We examined stomach contents in two smaller specimens from the Kapuas and found the following items: 148 mm, stomach full of macerated prawn exoskeleton, head capsule of aquatic? and abdomen of terrestrial? insects; 170 mm: head, dorsal fin, and pectoral girdle of catfish with strong, serrate fin spines (?*Leiocassis*) about 70-80 mm SL, operculate snail 6 mm (swallowed whole), cyprinid scale 7 mm. Stomachs of two largest specimens empty.

Distribution.—*Pangasius nasutus* has a disjunct distribution in Sumatra (Djambi, Batang Hari), Borneo (Barito, Kapuas, ?Labuk), and the Malay peninsula (Perak and Pahang). Weber and de Beaufort (1913:256) give additional Sumatran localities of Kwantan, Batu Ridial, and Indragiri for *P. nasutus*, but we have been unable to determine the basis for these records. Our material examined includes all museum specimens known to us.

Reports of *Pangasius nasutus* from Thailand (Smith 1945) and Indo-China are based on our new species *Pangasius conchophilus*, which has a less pointed snout, subterminal rather than inferior mouth, smaller teeth, larger eyes, and less stout fin spines.

***Pangasius nieuwenhuisii* (Popta)**
Fig. 2r

Neopangasius nieuwenhuisii Popta, 1904:180 (type locality, rivière Bo, Mahakam basin; Popta, 1906:30, pl. 1, fig. 3.

Pangasius nieuwenhuisi. Roberts, 1989:131,fig. 101b (dentition).

Material examined.—RMNH 7546, 400 mm, rivière B, Mahakam basin, A. W. van Nieuwenhuis (holotype).

Comparative description.—*Pangasius nieuwenhuisii*, known only from the holotype, belongs to a group of four species endemic to Borneo and distinguished from all other *Pangasius* in having palatal dentition consisting of a median tooth band. It apparently is most closely related to *P. humeralis*, the only other species with a greatly enlarged humeral gland and humeral spine. Direct comparison of the 400 mm holotype with two paratypes (312 and 389 mm) of *P. humeralis* (RMNH, Nov. 1989) revealed the following differences: eye more anterior and smaller, its diameter about two-thirds as large as in *P. humeralis*; Length of palatal tooth band one and a half times that in *P. humeralis*; and adipose fin of same length but

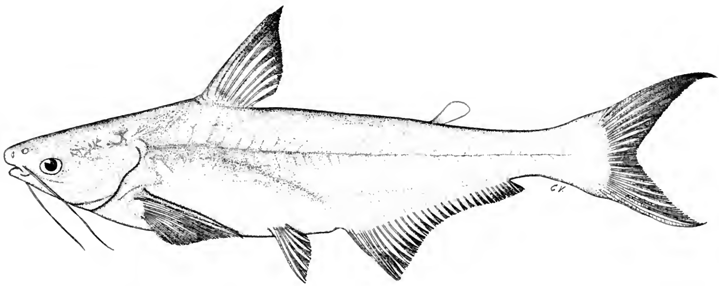

Fig. 19. *Pangasius pangasius*, 160 mm SL; Meghna River, Bangladesh (UMMZ 208434).

twice as large. The holotype has all fins uniformly dusky (possibly discoloration from preservative), with no indication of black pectoral fins characeristic of *P. humeralis*.

The holotype has gill rakers on first gill arch 7+12=19; anal fin rays 31?. A radiograph, difficult to interpret, shows 19?+28?=47? vertebrae.

Remarks.—The stomach of the holotype contains very hard seeds of higher plants, larger seeds crushed some to 9mm intact.

Distribution.—Known only from the Mahakam basin in eastern Borneo.

Pangasius pangasius (Hamilton)
Figs. 11, 2c, 19

Pimelodus pangasius Hamilton, 1822:163 (type locality estuaries of Bengal).

Pangasius buchanani Valenciennes *in* Cuvier and Valenciennes, 1840:45 (unwarranted replacement name for *P. pangasius*).

Pangasius pangasius godavarii David, 1962:151, fig. 3G (type locality Godavari River).

Pangasius pangasius upiensis Srivastava, 1968:97 (type locality River Rohini, Gorakpur, Uttar Pradesh).

Material examined.—CAS-SU 14123, 34862, 8:216-308 mm, Calcutta, A. W. Herre. April, 1937; UMMZ 208361, 6:45.7-132 mm, Meghna River near mouth of Gumpti River, W. Rainboth, Oct. 1977; UMMZ 208434, 21:66.1-161 mm, Meghna basin, Shabaspur River near Hatia Island, W. Rainboth, Oct. 1977; ZSM/CMK 5933, 106 mm, Assam, Dibru R., H. Bleher, 9 Nov. 1987; NMW 45455, 132 mm, Rangoon, L. Fea, 1885-88; NMW 45457, 261 mm, Irawadi, Rangoon, I. B. Za, Corvette Aurora (before 1896); NRM MAL/1934 485.4040, 4:124-137 mm, Rangoon; NRM MAL/1935.319.3286, 97.4 mm, Rangoon R., 1935.

Diagnosis.—*Pangasius pangasius*, type species of the genus *Pangasius*, is characterized by snout pointed in juveniles, more or less rounded in subadults and adults; mouth subterminal; palatal teeth in two palatine and two vomerine bands; gill rakers on first gill arch 23-28; pelvic fin rays 6; anal fin rays 31-34; vertebrae 42-45; body and fins without distinctive marks; males without filamentous fin extensions.

Distribution.—Large rivers and estuaries of Indian subcontinent and Burma; Ganges, Krishna?, Godavari; Irrawaddy. Widely introduced in Indian subcontinent and perhaps Burma for aquaculture. Reports from Thailand, Malaysia, and Indonesia are based on misidentifications of several species, including *P. hypophthalmus* in Thailand, perhaps *P. nasutus* in Malaysia, and *P. djambal* in Indonesia.

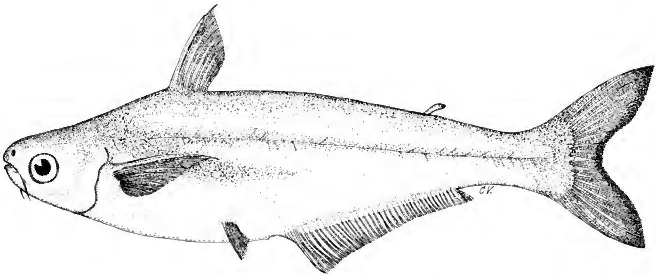

Fig. 20. *Pangasius pleurotaenia*, 219 mm SL; Mekong basin, Nongkhai (NIFI 2275).

Pangasius pleurotaenia Sauvage
Figs. 2f, 20

Pangasius pleurotaenia Sauvage, 1878b:235 (type locality Laos); Sauvage, 1881:169, pl. 8, fig. 6 (dentition); Sauvage, 1883:154 (Chao Phraya); Kottelat, 1984:813, figs. 7-8, table 1.
Pangasius cultratus Smith, 1931:25 (type locality Tapi River near Bandon, peninsular Thailand).
Pangasius fowleri Smith, 1931:28 (type locality Lopburi River, central Thailand).
Pteropangasius cultratus. Fowler, 1937:144, figs. 30-33; Smith, 1945:369.
Pangasius pleurotaenius Smith, 1945:361.

Material examined.—MNHN 9529, 135 mm, Laos (lectotype *P. pleurotaenia* designated by Kottelat, 1984:813); USNM 90306, 210 mm, Tapi R. near Bandon (holotype *P. cultratus*); USNM 90307, 141 mm, Chao Phraya at Bang Sai, Nov. 1923 (paratype *P. cultratus*); USNM 90309, 161 mm, Lopburi R. (holotype *P. fowleri*); USNM 109597, 178 mm, Meklong at Rajburi; NIFI 452, 2:230-250 mm, Kanchanaburi, Meklong basin; CAS 67209, 20:126-211 mm, Nakorn Sawan market, T. R. Roberts, 10-12 April 1989; NIFI 453, 3:60.0-97.0 mm, Ayuthya; NIFI 2264, 2:190-200 mm, Suphanburi, Tachin R., Chao Phraya basin; NIFI 451, 6:74.3-93.0 mm, Srichiangmai, Nongkhai province, Mekong basin; NIFI 2294, 6:42.3-119 mm, Nakorn Phanom, Mekong basin; NIFI 2275, 219 mm, Nongkhai market; CAS 67210, 143 mm, Khong Chiam market, T. R. Roberts, May 1989.

Notes on synonymy.—No additional specimens of *P. pleurotaenia* have been reported since its original description and subsequent report by Sauvage (1878b; 1881), and its status as a senior synonym of *P. cultratus* has not been recognized previously. Kottelat 1984:813 treated *P. pleurotaenia* as a valid species and alluded to its possible identity with *P. fowleri*, but not to *P. cultratus*. The lectoype of *P. pleurotaenia*, although in poor condition, agrees in all respects with *P. cultratus*, including possession of a complete abdominal keel; large eye; 17 gill rakers on first gill arch; 41 anal fin rays; 16+29=45 vertebrae; swim bladder extending posteriorly to above posterior third of anal fin; and large gap between palatal tooth bands of left and right sides. The abdomen is flacid and cut for its entire length immediately to one side of the abdominal keel. The holotype of *P. fowleri*, in excellent condition, has diagnostic characters of this species, including complete abdominal keel; large eye; 16 gill rakers on first gill arch; 42 anal fin rays; and swim bladder extending almost to end of anal fin base.

Diagnosis.—*Pangasius pleurotaenia* is distinguished from all other species of *Pangasius* by a well developed abdominal keel extends from vent to base of pectoral fins (in other species keel extending only from vent to base

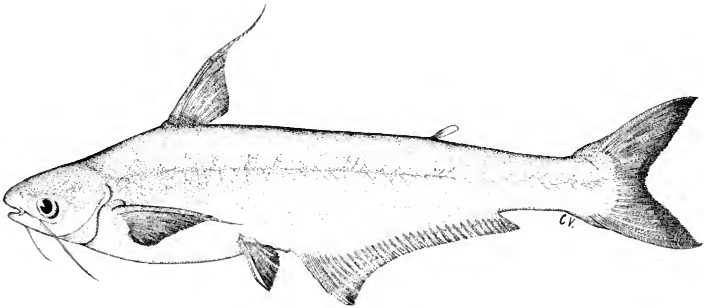

Fig. 21. *Pangasius polyuranodon*, 219 mm SL, male; Chao Phraya basin, Ayutthaya (NIFI 2270).

of pelvic fins); palatal teeth in two bands on each side, widely separated at midline; gill rakers on first gill arch 14-18; anal fin elongate, anal fin rays 39-46; vertebrae 43-45; swim bladder with three or four chambers, last chamber segmented and extending posteriorly to above end of anal fin base; midlateral and abdominal stripes sharply demarcated, separated on level with pectoral fin origin; caudal fin lobes usually with distinct stripes.

Size.—Maximum size to 30 cm standard length.

Distribution.—Pangasius pleurotaenia is found in the Mekong, Chao Phraya, Meklong and Tapi basins (Thailand, Laos, Kampuchea, and Vietnam).

Pangasius polyuranodon Bleeker
Figs. 1m, 2i, 21

Pangasius polyuranodon Bleeker, 1852a:425 (type locality "Bandjermassing, in fluviis").
Pangasius juaro Bleeker, 1852b:589 (type locality "Palembang, in fluviis").
Pseudopangasius polyuranodon Bleeker, 1862b:76, pl. 78.

Material examined.—BMNH 1863.12.4.79, 292 mm, Bleeker collection, no other data (labelled type *P. juaro*); RMNH 6855, 4:136-299 mm, Sumatra, Borneo, Bleeker collection, no other data (labelled *P. juaro*); RMNH 2929, 148 mm, Borneo [=Barito?], Schwaner, 1846; ZMA 115.742, 7:164-255 mm, Bandjermasin, H. A. Lorentz, May 1909; BMNH 1892.9.2.27, 168 mm, Limbang R., Borneo, A. Everett, May 1892; BMNH 1891.1.27.18, 463 mm, Baram R., Hose; BMNH 1978.3.20.319, 323 mm, R. Melinau, Gunong Mulu, Sarawak, J. Cramphorn, 1977; ROM 53694, 251 mm, Sungai Tinjar, Baram basin, M. H. Ang, 28 April 1981; CAS 49409, MZB 3681, 2:227-294 mm, Sintang, Kapuas basin, T. R. Roberts; CAS 67193, 2:189-192 mm, Sungai Belayan, Mahakam basin, eastern Borneo, M. S. Christensen, June 1982; ZMA 119.960, 387.9-108 mm, Batu Pangal, R. Kutei, Borneo, Siboga Exp., M. Weber, 1899; ZMA 115.744, 325 mm, Palembang, Sumatra; NMW 45468, 191 mm, Siam, Salmin, Jan. 1870; ANSP 60642, 4: 84.3-136 mm, Bangkok, de Schauensee, 1936; NIFI 2249, 5:152-174 mm, Bangsai, Chao Phraya basin; NIFI 2250, 3:184-230 mm, Bangsai; NIFI 2270, 220 mm, Bangsai; NIFI 2285, 397 mm, Bangsai; KUMF 1051, 85 mm, Paknam, Chao Phraya basin; KUMF 1050, 198 mm, Bangpakong basin; CAS 67211, 2:138-142 mm, Bangpakong R. near Prachinburi, T. R. Roberts, 22 March 1989; UMMZ 213960, 125 mm, Vam Ky Hon, My Tho, Vietnam; UMMZ 213962, 3: 72.1-107 mm, Vinh Long, Vietnam, W. Rainboth, June 1974.

Note on type specimens.—The original descriptions of *P. polyuranodon* and *P. juaro* are

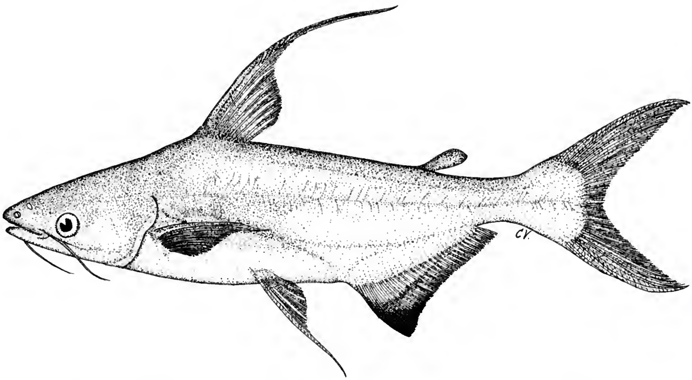

Fig. 22. *Pangasius sanitwongsei*, 129 mm SL; Mekong basin, Mukdaharn (NIFI 2248).

based on holotypes (speciminis unici 160'' and speciminis unici 336'', respectively). The holotype of *P. polyuranodon* might be the 136 mm RMNH 6855 Bleeker specimen; all other RMNH Bleeker specimens and the BMNH Bleeker specimen are too large. The holotype of *P. juaro* could be the 292 mm BMNH specimen, or one of the three larger specimens in RMNH 6855 (294, 299, and 299 mm).

Diagnosis.—*Pangasius polyuranodon* is a large, elongate species, with a short head (length 5.5-6.1 times in SL) and distinctive palatal dentition, consisting of a large, nearly square median vomerine tooth patch, and small lateral palatine toothplates. In some specimens the vomerine teeth are relatively hypertrophied and molariform, a condition not observed in other species. Dorsal and pectoral fin spines slender. Gill rakers on first gill arch 19-29. Anal fin rays 32-44. Vertebrae 46-50.

Geographical variation.—The number of anal fin rays is subject to geographical variation, with the highest counts, 39-44, in north Borneo. Specimens from Indo-China and Thailand have 32-37 anal fins rays, while the only two specimens available from the Mahakam basin in eastern Borneo both have 32 rays.

Size.—Attains about 80 cm standard length.

Distribution.—*Pangasius polyuranodon* is one of the most widely distributed species of *Pangasius*; its range includes Vietnam, Thailand, Malaysia, and Indonesia. In Thailand it is known from the lower reaches of the Chao Phraya and from the Bangpakong but not the Mekong or other rivers. It is known from the Mekong basin in Vietnam. It occurs in Sumatra, Java, and most major river basins of Borneo including Rejang, Kapuas, Barito, and Mahakam.

Pangasius sanitwongsei Smith
Figs. 1n, 2h, 22

Pangasius sanitwongsei Smith, 1931:29, figs. 13-14 (type locality Menam Chao Phraya at Koh Yai, central Siam [near Ayuttaya]); Smith, 1945:363, fig. 82.

Pangasius beani Smith, 1931:26 (type locality Lopburi River).

Material examined.—USNM 90308, 153 mm, Lopburi R. near Ayuthia (holotype *P. beani*); KUMF 173, 180 mm, Lopburi (paratype *P. beani*); KUMF 1052, 193 mm, Nakorn Sawan, Chao Phraya basin; NIFI 439, 145 mm, Nongkhai, Mekong basin; CAS 67212, 3:60.3-118 mm, Mekong R. at Bung Kla, T. R. Roberts, 7 July 1985; CAS 67213, 149 mm, Mekong R. at Bung Kan, T. R. Roberts, 3 Jan. 1989; NIFI 2252, 2:58-79 mm, Nakorn Phanom, Mekong basin; NIFI 2074, 40:60-109 mm, Mukdaharn, Mekong basin; NIFI 2248, 179 mm, Mukdaharn; NIFI 435, 103 mm Ubol, Mekong basin.

Note on holotype.—The original description was based on a single specimen, the holotype, "61.6 cm long." Figure 13, accompanying the original description, is based on the holotype; we confirmed this by examination of the original illustration by Luang Masya (currently deposited in the Fish Collection at NIFI). The holotype originally was deposited in the "Siamese Department of Fisheries" (Smith 1931:30). Our efforts to locate this type have been unsuccessful. So far as we have been able to determine, it is not present in the Department of Fisheries, NIFI, or Kasetsart (KUMF). Possibly it will be located at Kasetsart. In the 1950's, when the Department of Fisheries moved to its new location on Radjadamnoern Nok, all or most of the Smith specimens were transferred to Kasetsart.

Notes on synonymy.—Although both nominal species were described in the same article by Smith, *P. sanitwongsei* was based on a large adult (figured), whereas *P. beani* was based on a 153 mm juvenile (not figured). In subsequent publications the species has been identified consistently as *P. sanitwongsei*, and no additional specimens of *P. beani* have been reported. Thus, while *P. beani* has page priority over *P. sanitwongsei*, as first revisors we select *P. sanitwongsei* as the senior synonym with nomenclatural priority.

Diagnosis.—*Pangasius sanitwongsei* has a broader head and mouth than any other species of *Pangasius*. Dorsal, pectoral, pelvic, and anal fins with filamentous extensions. Distal portion of anterior anal fin rays dusky or black; some individuals with a pale or white humeral spot not seen in any other species of *Pangasius*; gill rakers on first gill arch 16-21; vertebrae 50-52, with more compressed centra than any other species of *Pangasius*.

Food habits.—Little is known about food of this species. Presumably it feeds mainly on fish. Two juveniles of 60 and 80 mm SL from Nakorn Phanom had small fishes only in their stomacks. The larger fish had eaten three *Pangasius macronema* of 15-20 mm SL, one *Belodontichthys* (silurid catfish) of 20 mm, and one small cyprinid. Larger individuals will take carcasses of fowl or dogs (commonly used for bait).

Size.— Attains 2.5 m or 3 m standard length and 300 kg. Because of its large size and rapid growth, this species also has potential use in aquaculture.

Distribution.—*Pangasius sanitwongsei* occurs only in the Chao Phraya and Mekong basins (Thailand, Laos, Kampuchea, and Vietnam).

Helicophagus Bleeker

Helicophagus Bleeker, 1858a:45 (type species *Helicophagus typus* Bleeker, 1858, by monotypy).

Diagnosis.—*Helicophagus* differs from all other pangasiids in having a relatively elongate snout and narrow mouth; this involves greater elongation of the ethmoid portion of the skull and more narrow transverse (or lateral) ethmoid processes and prevomer. Palatal dentition consisting of two round or oval tooth patches. It further differs from all or nearly all other species except *P. macronema* in having relatively long mandibular barbels, and from all other species except *P. conchophilus* in feeding mainly on molluscs (*Helicophagus* does not appear to be particularly closely related either to *P. macronema* or *P. conchophilus*).

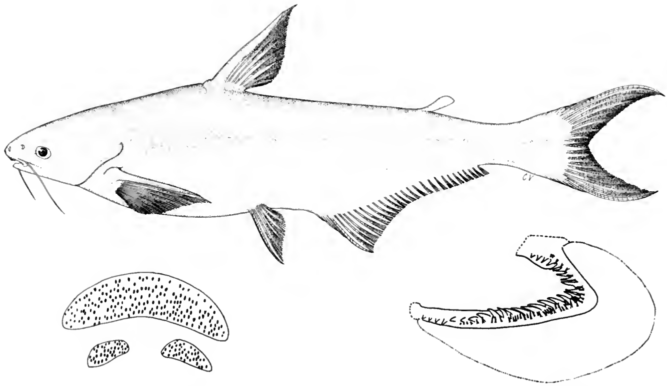

Fig. 23. *Helicophagus typus*, 362 mm SL; Musi basin, Palembang (ZMA 120.525). Left insert, palatal teeth (362 mm); right insert, first gill arch (377 mm).

Key to species of *Helicophagus*

1a. Premaxillary teeth in an undivided, curved band; gill rakers on leading edge of first gill arch 27-30; numerous small gill rakers on anterolateral face of first gill arch; anal fin rays 30-31 .... ***H. typus***

1b. Premaxillary teeth in two quadratic patches, one on each side of jaws, clearly separate at midline; gill rakers on leading edge of first gill arch 8-12; no small gill rakers on anterolateral face of first gill arch; anal fin rays 38-42 .... ***H. waandersii***

Helicophagus typus Bleeker
Fig. 23

Helicophagus typus Bleeker, 1858a:45 (type locality Palembang, in flumine Mussi); Weber and de Beaufort, 1913:252.

?*Helicophagus typus*. Hardenberg, 1948:412 (Bandjermassin, SE Borneo; specimens not examined by us).

Material examined.—BMNH 1863.12.4.118, 177 mm, Palembang (holotype); ZMA 120.525, 2:362-377 mm, Palembang, Salm, 1908.

Remarks.—The fate of the many of the Indonesian specimens collected by the late J. Hardenberg, including those he identified as *H. typus* from Borneo, is unknown. Many, including types of new species described by Hardenberg, were deposited in the Pasar Ikan (fish market) Laboratory at Tandjung priok, Jakarta, and may have been taken by the Japanese, as related by Hardenberg to Marinus Boeseman (pers. comm. M. Boeseman, 22 Feb. 1990).

Comparative description.—Refer to key above. *Helicophagus typus* is the only pangasiid in which small gill rakers have been observed on the anterolateral face of the first gill arch. *Pangasius hypohthalmus* has rakers of similar size alternating with relatively large or "normal" rakers on the leading edge of the first gill arch. In *H. typus* the small or auxilliary rakers do not alternate with the rakers on the leading edge of the arch, but are concentrated near the

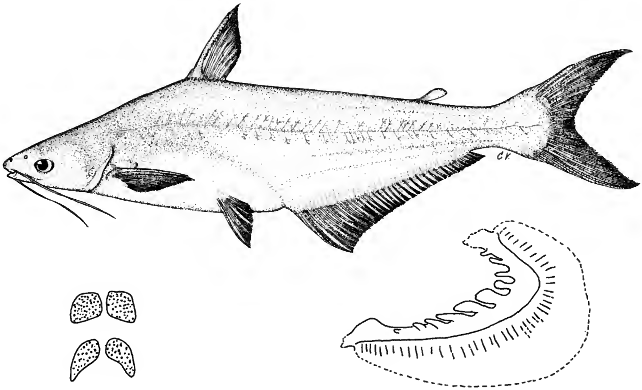

Fig. 24. *Helicophagus waandersii*, 201 mm SL; Mekong River, Nongkhai (NIFI 2287). Left insert, palatal teeth (244 mm); right insert, first gill arch (244 mm).

angle of the arch on the anterolateral margin. These small rakers are not included in the count of rakers on the first gill arch.

The swim bladder has three chambers. The first or anterior chamber is oval and occupies the anterior two-thirds of abomen; the second chamber has been removed. The third is a nearly uniform cylinder 65 mm long extending from just before anal fin origin to middle of caudal peduncle. Vertebrae 18+26=44.

Food Habits.—The holotype had the stomach entirely filled with hundreds of small gastropods (Bleeker 1858a:46; Bleeker 1862b:78). The stomach has since been removed, but numerous small gastropods are scattered about the abdominal cavity and mesenteries; the largest are about 0.8 mm.

Distribution.—*Helicophagus typus* has been reported only from Sumatra and southeast Borneo. The current status of populations of *H. typus* is unknown; the last known specimens that can be positively identified (from Palembang) were collected in 1908.

Helicophagus waandersii Bleeker

Figs. 1p, 24

Helicophagus waandersii Bleeker, 1858b:175 (type locality Palembang); Weber and de Beaufort, 1913:253, fig. 102; Hora, 1937:256; Smith, 1945:371.

Material examined.—BMNH 1863.12.4:89, 277 mm, Palembang (holotype); ZMA 120.519, 3:192-265 mm, Batang Hari, Djambi, P. E. Moolenburgh, 22 Dec. 1909; NIFI 2287, 201 mm, Mekong R., Nongkhai; CAS 61908, 50:52.4-238 mm, Ubon Ratchatani market, T. R. Roberts, 2 July 1985; MNHN 9632, 347 mm, Laos Siamois, Jullien, 1874; MNHN B.307, 472 mm, Mekong, Harmand, 1876; MNHN 1987-139, 295 mm, Cambodge.

Diagnosis.—Refer to preceding key and account of *H. typus*. The holotype has swimbladder with three chambers. Two anterior chambers in abdomen, posterior chamber extending from just anterior to anal fin origin above four-fifths of anal fin base. Vertebrae 16+29=45.

Food Habits.—Many of the specimens we

have seen, including many from Thailand not included in the list of material examined, have stomach more or less filled with molluscs, always or almost always bivalves. Four specimens 8-15 cm SL from the Menam Mun, captured in June-July 1985, had fed exclusively on clams, mainly *Corbicula* (Corbiculidae) but also *Physunio* (Amblemidae) [identifications by Wantana Yoosuk].

Distribution.—Helicophagus waandersii is known only from Sumatra and the Mekong and Chao Phraya basins.

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Avifauna of the Río Manití and Quebrada Vainilla, Peru

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ABSTRACT.—A total of 328 avian species were recorded at two neighboring localities on the south bank of the Río Amazonas, Depto. Loreto, Peru during July-August 1983. Field work at both sites was concentrated in primary, *terra firme* forest. A complete species list with relative abundance designations is presented. Additional information is given for 18 poorly known species. Our results are compared to two other well-studied sites in southern Amazonian Peru, both of which have more extensive river-created habitats and species associated with them. [Amazonian Peru, avifauna, *terra firme* forest]

The lowland tropical rain forest of Amazonia habors the most diverse avifauna on the planet (Meyer de Schauensee 1966; Haffer 1974). The past two decades has witnessed an increase in inventory field work that has helped elucidate the status and distribution of this avifauna. The data from these inventories support the interpretation that the complexity of Amazonian bird distributions reflects both the heterogeneity of lowland tropical forest and historical forces affecting speciation. For example, the avifauna of Amazonian *terra firme* forest shows high levels of regional species diversity associated with rivers (e.g., Sick 1967, Capparella 1988, *in press*) and putative refugia (Haffer 1987). Furthermore, numerous species known originally from a few scattered localities actually have extensive distributions. Con-

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versely, many species originally thought to be uniformly distributed over Amazonia actually have patchy ranges because of their specialized habitat requirements (e.g., bamboo; Parker 1982). Despite this increase in interest, a recent compilation (Vuilleumier 1988) of published species lists includes only six for western Amazonia that are reasonally comprehensive (i.e., included 300+ species); another (Parker and Remsen 1987) was published subsequently.

Additional comprehensive bird lists are needed from throughout Amazonia to properly depict the regional species diversity in this complex biome. These lists provide the fundamental data base for analyses by biogeographers (e.g., Haffer 1974,1985; Cracraft 1985; Cracraft and Prum 1988) and conservationists (e.g., Simberloff 1986).

We present results from a survey of two neighboring localities on the south bank of the Río Amazonas in northeastern Peru. This is the first published list for a Peruvian site south of the Río Amazonas and north of the Río Yavarí. The combined species total is 328 (see Appendix - undoubtedly a number of permanent resident species were overlooked), and additional information is given for 18 poorly-known species. Our findings are compared with two other intensively surveyed lowland, south bank sites in Peru to determine the extent of avifaunal similarity. Comparisons with the avifauna on the north bank will be presented in a subsequent paper.

SITES

Two sites located less than 15 km apart on the south bank of the Río Amazonas, Depto. Loreto, Peru, were surveyed in 1983. The sites were located as precisely as possible on a Landsat image (scene identification # 8224514160500) and compared to a map of Loreto issued by the Instituto Geographico Militar in 1973, from which latitude and longitude were determined (Fig. 1). Both areas consisted of relatively undisturbed *terra firme* forest on level terrain between 100-125 m above sea level. At both sites the forest was rather

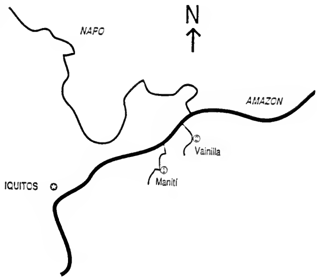

Fig. 1. Approximate locations of the Río Manití and Quebrada Vainilla sites. Map constructed from Landsat image.

open with relatively few arboreal vines and lianas, and no bamboo. The width of the Manití and Vainilla rivers near our camps were ca. 15 and 10 m, respectively. Neither area had any lagoons or other large bodies of water. However, at each site there were a few small forest streams containing little water. Very little rainfall fell during the period of investigation, which coincided with the dry season.

The Academy of Natural Sciences party (Robbins, Ridgely, G. Castro, T. Pedersen, A. Villavisensio) surveyed forest on the east bank of the Río Manití at the village of Santa Cecilia (ca. 03° 33' S, 72°53'W), approximately 5 km southeast of the Amazon, between 3-18 August 1983. Government plans at that time called for ca. 210,000 hectares of primary forest to be cleared for production of African Oil Palms (a plan that has since been abandoned). A 1.5 km strip of forest east of the Manití had already been cleared prior to our arrival, and this was the area in which most second-growth species were recorded. A grid of narrow lanes had been laid out in the section of primary forest that was surveyed; otherwise the forest was relatively undisturbed. Mist nets (15-20/day; each 12 m in length; opened at dawn and closed by late

morning), shotguns and daily observations (mainly by Robbins and Ridgely) with recording equipment were used to census birds. Most observations were made between dawn and late morning (ca. 11:00). Most afternoons were spent preparing specimens. There was little rainfall during the period, and by the end of our stay the Rio Manití was so low that it was difficult to navigate by motorized canoe.

The Louisiana State Museum of Natural Science party (Capparella, Cardiff, T.J. Davis, D.L. Dittmann, T.C. Maxwell, M. Sanchez S., A. Urbay T.) worked an area ca. 5 km south of the Río Amazonas, on the east bank of the Quebrada Vainilla (ca. 03° 32'S, 72° 44'W), between 13 July and 11 August 1983. The terrain was gently rolling in the immediate vicinity of the stream but quickly flattened out to the east. Most collecting effort was directed in the interior *terra firme* forest with less time spent sampling clearings (small man-made patches scattered throughout the forest), second-growth (located within 0.5 km of the stream) and stream edge. A trail system extended several km into the interior of the forest. Mist nets (mode of 62/day, most 12 m in length, opened dawn to dusk), shotguns, and daily observations were used to census birds. On most days, one member of the party would remain in camp all day (rotated among members); the other members spent from dawn to early or mid-afternoon collecting and observing. The remainder of the day and evening was spent preparing specimens. During this period, water levels in the Vainilla fluctuated greatly depending on rainfall, virtually drying up on several occasions.

METHODS

Although the Manití and Vainilla sites are treated as one due to their close proximity and habitat similarity, the following caveats should be noted. First, there was a difference in the type and intensity of censusing at the two sites. Fewer nets and people were involved in the census at the Manití than at the Vainilla site. Sound recording equipment was used only at the Manití site. Furthermore, the two groups overlapped temporally by only six days and members of the different groups did not visit each others' site to get a "feel" for similiarities and differences. Despite these caveats, we believe the coarse estimates of abundance and site comparisons made are informative due to 1) the extensive overlap in our species lists, 2) comparison of our impressions and notes, and 3) the experience of T. A. Parker III, who visited each site for about a day and felt that there were not any major differences in habitat.

Classification and species order follow Meyer de Schauensee (1970), except for the tyrannids, piprids and cotingids, where we follow Traylor (1979). For species included in the sixth edition of the A.O.U. Check-list (1983), we have adopted English and scientific names (but not phylogenetic order), except for the puffbirds (Bucconidae) which follow Meyer de Schauensee (1970). Study skins are deposited at the Academy of Natural Sciences, Philadelphia (ANSP), Louisiana State University Museum of Natural Science, Baton Rouge (LSUMZ), and the Museo de Historia Natural "Javier Prado," Lima, Peru (the latter reported under the ANSP or LSUMZ catalog number under which they were initially cataloged). All anatomical specimens and tissue samples are housed at LSUMNS. Robbins' sound recordings obtained at the Río Manití are deposited at the Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York (LNS). Referenced photographs are deposited at VIREO, ANSP.

Species accounts include natural history observations, general remarks and specimen data. The latter includes museum catalog number, gonadal measurements, mass (=weight), soft part colors and stomach contents. Gonadal dimensions are rounded to the nearest 0.5 mm. Mass of specimens less than 10 g is reported to the nearest 0.1 g, mass from 10-30 g is rounded to 0.5 g, and mass greater than 30 g is rounded to the nearest gram. Ranges are given for gonadal dimensions and mass when more than two specimens are reported. Unless otherwise noted, soft part colors apply to both sexes.

SPECIES ACCOUNTS

Zebrilus undulatus
Zigzag Heron

A female of this rarely encountered species was mist-netted on 12 August near a stagnant pool along a largely dry, forest stream at Santa Cecilia. The plumage of our bird fits the adult plumage described in Hancock and Kushlan (1984). Blake (1977) describes the irides as "black, sometimes (?) with a yellow inner ring." The irides of the Manití female (see description; VIREO r08/1/007) closely match those of an adult female recently collected in Bolivia (Depto. Santa Cruz; LSUMZ 136695). However, two other adult females in the LSUMNS collection have irides color described as "dark brown" (LSUMZ 42681) and "yellow" (LSUMZ 71899). In Peru, this heron is known from less than ten specimens.

To our knowledge, the voice of *Zebrilus* has never been described; P. Greenfield was the first to identify it from work in Ecuador. As heard subsequently by Ridgely in eastern Ecuador, the only vocalization known to be given by this species is a deep, loud, almost mournful "ooooh" with distinctly hollow quality (thus somewhat dove-like), given at 6-7 second intervals. Vocalizing birds perched inside *varzea* forest at the edge of small lakes and sluggish streams at heights varying between 2-6 m above the ground. Vocalizations were heard most often in the late afternoon (16:00 to 18:00 hrs), less often in the early morning (06:00-08:00 hrs), and occasionally at night.

Specimen data: 1 female (ANSP 176006), ovary 6 x 5 mm, ova minute; 123 g; irides dark brown, with a thin inner ring of yellow, maxilla blackish-brown, mandible horn, tarsi yellow; stomach contained a leech, ca. 140 mm in length.

Leucopternis kuhli
White-browed Hawk

Four individuals of this poorly known species were collected in the forest interior. One was captured in the bottom rung of a mist net, apparently trying to rob captured birds. Cardiff observed one capture a lizard on the forest floor; this bird (LSUMZ 114578) also had a small snake in its stomach. There is a discrepancy in soft part colors between the literature and our specimens. Brown and Amadon (1968) and Blake (1977) state that the irides and tarsi are yellow. Our four specimens (including photos of ANSP 176007 alive, VIREO rO8/1/004-006) had brown or reddish-brown irides and orange tarsi in life. Furthermore, the irides of a bird photographed in the hand from the eastern portion of this species' range (Belém, Brazil; Ridgely, VIREO r10/7/001-002) are also brown.

Some conservationists have expressed concern about the status of this species. Due to its relatively large distribution (from the south bank of the Río Amazonas west to the Río Ucayali of Peru, south to northern Bolivia, and east to eastern Pará, Brazil), and the extensive pristine forest remaining in its range, we do not believe this hawk is currently threatened.

Specimen data: 2 males (LSUMZ 114578; ANSP 176007), testes 7 x 2 mm, 8 x 1 mm; 315-330 g; 1 female (LSUMZ 114579), ovary 13 x 5 mm; 385 g; 1 unsexed alcoholic (LSUMZ 114338), 355 g; soft part colors (see above); stomachs contained bird, mammal, snake and beetle remains.

Galbula cyanicollis
Blue-cheeked Jacamar

We follow Haffer (1974) in recognizing this taxon as a species separate from *G. albirostris*. *Galbula cyanicollis* is known from south of the Río Amazonas from its mouth west to at least as far as the area between the lower Río Ucayali and Río Huallaga (south bank of the Río Marañon, along Río Samiria, ANSP unpubl. data) in northeastern Peru. The Manití/Vainilla series are extremely similar in plumage to birds from further west (Río Samiria), thus supporting Haffer's (1974) assertion that birds in the western part of this species' range have less blue on the cheeks and malar region than do

individuals from much farther east. Eighteen of the 24 LSUMZ specimens were netted, and the remaining six were shot from 4-10 m above the ground. One of these was collected from a middle-story mixed-species flock.

Specimen data: 18 males (LSUMZ 114745, 114747-53, 114756-60, 118355, 118357, 118359; ANSP 176039-40), testes 3.5 x 2 - 7 x 4 mm; 20-26 g; 7 females (LSUMZ 114385, 114744, 114746, 114754-5, 118356, 118358), ovary 5 x 3 - 7 x 4.5 mm; 20-27 g; irides brown, bill yellow with black culmen, orbital skin yellow, tarsi and feet orange; stomachs contained insect parts.

Malacoptila rufa
Rufous-necked Puffbird

As with most members of this genus, very little is known about this puffbird's natural history. This inconspicuous species was encountered with surprising frequency. Individuals were observed quietly perched from 1-3 m above the forest floor. Although we failed to identify any vocalizations of this species, gonadal data indicate that it was breeding, as all adult females (based on 100 % skull pneumatization, except one which had the skull only 70 %) had enlarged ovaries. One netted female, whose oviduct was 15 mm in diameter, apparently had laid an egg just prior to capture. Another female, that laid an all white egg (28 x 21 mm) while being held in a bag for photographing at Río Samiria (23 August 1985; ANSP 177711), also had a dilated oviduct. Furthermore, two birds (one collected, male, ANSP 176044) had fresh mud on the tips of their bills, presumably indicating fresh excavation of holes in the ground.

Specimen data: 10 males (LSUMZ 114780, 114782, 114784, 114787-8, 118364, 118366-7, ANSP 176043-4), testes 2 x 1 - 6 x 4 mm; 39-55 g; 8 females (LSUMZ 114781, 114783, 114785-6, 114789-90, 118365; ANSP 176042), ovary 3 x 1 - 25 x 25 mm; 41-58 g; 2 unsexed alcoholics (LSUMZ 114388-9); 51 g; irides red, bill bluish-gray with black tip, tarsi and feet dull olive-brown; stomachs contained beetles, grasshoppers, army ant, caterpillars, a tarantula and unidentified insects.

Nonnula rubecula
Rusty-breasted Nunlet

We encountered this species only twice without the aid of mist nets. One individual was observed perched quietly ca. 20 m above the ground at the edge of primary forest. After a few minutes it disappeared into the forest interior. Another individual was collected from a perch ca. 9 m above the ground in primary forest.

Specimen data: 2 males (LSUMZ 114795, 114797), testes 3 x 2 - 3.5 x 1.5 mm; 17-19 g; 3 females (LSUMZ 114794,114796,114798), ovary 4.5 x 3.5 - 9 x 5 mm, ovum minute; 17.5-18.5 g; irides brown, maxilla black, mandible bluish-gray or silvery-gray with black tip, tarsi gray.

Xenops milleri
Rufous-tailed Xenops

Meyer de Schauensee (1966) lists a single locality for this species in Peru (Depto. Loreto; Chamicuros). Subsequently, it has been reported as fairly common at the Tambopata Reserve (Depto. Madre de Dios, 12° 50'S, 69°16'W) in southeastern Peru (Parker 1982). Four specimens were taken from canopy mixed-species flocks at Vainilla, and it was also recorded in canopy flocks at the Manití.

Although the above relatively large gap between our records and those from Tambopata may give the impression that this canopy dweller has largely been overlooked, Parker (pers. comm.) believes it is at best only patchily distributed in lowland forest in western Amazonia from eastern Colombia southward to the Peru/Bolivia border.

Specimen data: 3 males (LSUMZ 115143, 115145, 118407), testes 1.5 x 1 - 3.5 x 5 mm; 12.5-13 g; 1 female (LSUMZ 115144), ovary 6 x 3 mm; 12.5 g; irides dark brown, maxilla black, mandible leaden blue, tarsi and feet olive; stomachs contained insect fragments.

Sclerurus rufigularis
Short-billed Leafscraper

We netted 11 individuals of this inconspicuous ground-dweller. This leafscraper has only recently been found in Peru (Cardiff 1983); our records represent the second locality for the country.

The Manití/Vainilla series appear to match two specimens of the nominate race from Pará, Brazil (ANSP 80592-3). The Pará specimens are slightly more rufescent on the belly and abdomen, but this may be the result of postmortem changes in plumage color ("foxing"), as these specimens were collected in 1926.

Specimen data: 7 males (LSUMZ 115152-6; ANSP 176110,176112), testes 6 x 5.5 - 11 x 5 mm; 21-22 g; 3 females (LSUMZ 115151, 115157; ANSP 176111), ovary 7 x 3 mm; 21 g; 1 unsexed alcoholic (LSUMZ 114442); 21 g; irides dark brown, maxilla dark brown or black, mandible gray or pinkish-white at base, black at tip, tarsi pinkish-brown or dark gray; stomachs contained insect fragments.

Myrmotherula sclateri
Sclater's Antwren

This species was overlooked until D. Stotz re-identified a specimen from the Manití that was originally catalogued as *M. brachyura*. Stotz and Parker also identified this species in the background in many of the sound recordings of canopy mixed-species flocks. This species has been recorded at six additional Peruvian sites (all south of the Río Amazonas and east of the Río Ucayali) and in northern Bolivia (Deptos. Pando and La Paz; Parker and Remsen 1987).

Specimen data: 1 female (ANSP 176205), ovary 5 x 3 mm, ova minute; 8.0 g; irides brown, maxilla black, mandible pale gray, tarsi gray; stomach contained insect parts.

Neoctantes niger
Black Bushbird

The two specimens netted at Vainilla represent only the second locality for this species south of the Río Amazonas in Peru. Terborgh et al. (1984) netted and photographed this species at Manu (11°55'S, 77°18'W).

Specimen data: 1 female (LSUMZ 115206), ovary 6 x 3; 29 g; 1 unsexed alcoholic (LSUMZ 114435); 28.5 g; irides brown, maxilla dark gray with bluish-gray tomia, mandible bluish-gray with dark gray tomia, tarsi and feet dark gray.

Terenura humeralis
Chestnut-shouldered Antwren

As Parker and Remsen (1987) reported, our three specimens taken by Cardiff from canopy mixed-species flocks at Vainilla represent only the second specimen locality for Peru. The other site is on the north bank of the Río Amazonas at Pebas, Depto. Loreto (Zimmer 1932). However, Parker (1982) found it to be "an inconspicuous member" of forest canopy mixed-species flocks in southeastern Peru (Tambopata Reserve and Manu), and it has recently been found in northern Bolivia (Depto. Pando; Parker and Remsen 1987).

Specimen data: 2 males (LSUMZ 115331, 115333), testes 6 x 3 - 6 x 4; 7.0 g; female (LSUMZ 115332), ovary 5 x 2.5 m; 7.8 g; irides dark brown, maxilla black, mandible, tarsi and feet leaden blue; stomachs contained insect fragments.

Hypocnemis hypoxantha
Yellow-browed Antbird

This species was fairly common in areas with reduced forest canopy (e.g., treefalls, small clearings). Birds were seen singing and foraging within 5 m of the ground (usually between 2-3 m) in relatively dense understory. Vocal activity and gonadal data indicate that it was breeding.

Hilty and Brown (1986) describe the song as

a "fast (2 sec), sharp *queeque-queeet* repeated every 3-4 sec." Songs of males recorded under natural conditions at Manití were longer in duration, usually 5-6 sec, and consisted of 7-14 notes (usually 12). The initial 2-3 notes, occasionally the first 4-5, had a loud, almost emphatic ringing quality (not unlike the introductory notes of many *Myrmeciza* antbird songs). As the song progressed, the notes became more raspy, and the final three or four notes were very guttural and drawn out.

Specimen data: 6 males (LSUMZ 115394-5,115397,118437; ANSP 176213, 176215), testes, 3 x 1 - 3 x 2 mm; 10.5-12.5 g; 6 females (LSUMZ 115392-3,115396,118438, ANSP 176214,176216), ovary 4 x 2 - 15 x 9 mm; 10-13.5 g; irides brown, maxilla black, mandible black (males) or bluish-gray (females), tarsi and feet bluish-gray; stomachs contained insects fragments.

Conopophaga aurita
Chestnut-belted Gnateater

Until our work, this poorly known gnateater had been collected at less than a half dozen localities in Peru (Zimmer 1931; LSUMZ unpubl. data; specimen in Field Museum of Natural History, Chicago, fide T. Schulenberg). We found it to be uncommon, with all observed birds perched on thin branches or rootlets within 1.5 m of the forest floor. On one occasion, a solitary bird sang while perched perpendicular to a horizontal perch, ca. 0.5 m above the ground. It then flew ca. 4 m to a vertical limb where it perched briefly before disappearing. The song consisted of 5-6 relatively thin, high-pitched notes delivered in rapid succession. Most of the females showed signs of breeding; one female (LSUMZ 115605) collected on 26 July, whose oviduct was 9 mm in diameter, apparently had just laid an egg.

Specimen data: 14 males (LSUMZ 114464, 115595, 115597-600,115606-8,118462, 118464-5; ANSP 176218-9), testes 2 x 1 - 8 x 4 mm; 23-28 g; 7 females (LSUMZ 115596,115601-5,118463), ovary 6 x 3 - 20 x 15; 24-31 g; irides brown, bill black, tarsi and feet gray; stomachs contained insects.

Myiopagis caniceps
Gray Elaenia

Prior to our work this little-known, sexually dimorphic flycatcher had been collected at only three widely separated localities in eastern Peru (Zimmer 1941; Traylor 1979). However, Parker (pers. comm.) stated that this species is widespread throughout western Amazonian Peru, both north and south of the Río Amazonas. A male was taken at the Manití site at the edge of primary forest from a mixed-species flock over 15 m above the ground, and a female at Vainilla was shot from a canopy mixed-species flock.

Specimen data: 1 male (ANSP 176243), testes 5 x 2 mm; 9.5 g; 1 female (LSUMZ 115989), ovary 7 x 3 mm, lg. ovum 2 mm; 11 g; irides brown, bill and tarsi black; stomachs contained insects.

Lophotriccus vitiosus
Double-banded Pygmy-Tyrant

Our series of seven specimens are clearly referrable to the race *congener*, the first record of this subspecies west of the type locality (São Paulo de Olivença, Rio Solimôes, Brazil; Traylor 1979). The Río Ucayali may separate *congener* from the nominate race, which is known from the Deptos. of San Martín, Ucayali and Huánuco. Males (confirmed by collecting) were heard giving a buzzy trill, *"tr'E'E'E'E'E'E"* (after Hilty and Brown 1986), throughout the day from perches 4-8 m above the ground near openings within the forest.

Specimen data: 3 males (ANSP 176252-4), testes 5 x 2.5 - 6 x 3 mm; 7-8 g; 4 females (LSUMZ 115983-6, 118514), ovary 3 x 1 - 6 x 4 mm; irides buff-white or yellowish-white, maxilla dark gray, mandible dark gray with whitish-edges and base, tarsi pinkish-gray; stomachs contained insects.

Attila citriniventris
Citron-bellied Attila

Previously, this species had been recorded only once south of the Río Amazonas, east of the Río Ucayali (Tefe, Brazil; Traylor 1979). At our sites it was fairly common, and due to its loud and often repeated song, it was conspicuous in the upper story and canopy of primary forest. The description of the song of birds from Venezuela (P. Schwartz, in Hilty and Brown 1986) accurately depicts the voice of the birds at Manití/Vainilla. Males typically gave a seven, occasionally only five, noted song, about 2-3 sec in duration.

Specimen data: 2 males (LSUMZ 115891, ANSP 176270), testes 6 x 2 and 5.5 x 2 mm; 33 and 38 g; 1 female (LSUMZ 115890), ovary 8 x 4 mm; 30 g; 1 unsexed alcoholic (LSUMZ 114495); 32 g; irides reddish-brown, maxilla gray or dark brown, mandible pale horn or light brown, tarsi and feet light gray; stomachs contained insects.

Conopias parva
White-ringed Flycatcher

This species was fairly common, with 3-4 birds heard daily at openings in the forest canopy. It was not detected at the Vainilla site, where it was likely overlooked. The single specimen is the first for Peru, although there is a sight record of 2+ birds on 9 June 1979, ca. 12 road km east of Nuevo Andoas, Río Pastaza, Depto. Loreto by E. Willis (*in litt.*). Prior to these records, the closest known locality was in Vaupés (Mitú), Colombia, some 650 km to the north (Hilty and Brown 1986).

Specimen data: 1 male (ANSP 176273), testes 13 x 5 mm; 23 g; irides brown, bill and tarsi black; stomach contained 1, large chestnut-colored fruit, ca. 13 x 5 mm.

Icterus cayanensis
Epaulet Oriole

Icterus cayanensis and *I. chrysocephalus* have been reported to hybridize along the Río Amazonas as close as ca. 550 km to the east of our study sites (Tonantins, Brazil; Blake 1968). The birds observed at the Manití site (5-10 birds; 1 specimen), however, were typical of *cayanensis* in having an entirely black cap.

Specimen data: 1 female (ANSP 176299), ovary 6 x 3 mm; 39 g; irides dark brown, bill and tarsi black; stomach contained insects.

Lamprospiza melanoleuca
Red-billed Pied Tanager

Until our work, *Lamprospiza* was unknown from north of the upper Río Ucayali in Peru, or west of the mouth of the Rio Madeira, Brazil (Meyer de Schauensee 1966; Isler and Isler 1987). Recently, this species has also been found in the Río Shesha area, east of Pucallpa, Depto. Ucayali (LSUMNS unpubl. data). This species is probably widespread but locally distributed from the mouth of the Amazon westward to the Río Ucayali.

On at least three occasions birds (1-3 individuals) were seen gleaning insects from small leaves in the canopy over 40 m above the forest floor. Although no specimens were obtained, sound recordings were made of individuals giving high-pitched call notes (LNS 37401).

COMPARISON OF THE MANITÍ/VAINILLA AVIFAUNA WITH TWO OTHER PERUVIAN LOWLAND SITES

To characterize the regional species diversity in western Amazonia, we have compared our list with the two most extensively surveyed sites in western Amazonian Peru (both areas further to the south): 1) Explorer's Inn, Tambopata Reserve (12°50'S, 69°16'W; Parker 1982; Parker, pers. comm.) and 2) Cocha Cashu Biological Station, Manu National Park (11°55'S, 77°18'W; Terborgh et al. 1984). Two groups of birds are excluded from this comparison: 1) water-associated species (e.g., Ciconiiformes, Charadriiformes, kingfishers), because this habitat was either not present (e.g., oxbow lakes) or was not extensively surveyed at Manití/Vainilla; and 2) North American

migrants, because they were absent during the time of our survey at Manití/Vainilla. We have exercised caution in these comparisons because the Manití/Vainilla site was surveyed for a short period (in comparison with the years spent at Tambopata and Manu) at only one season (height of the dry season). These biases make it more likely for a species to be improperly recorded as absent from the Manití/Vainilla than the reverse. Therefore, the most reliable comparison of differences is between those species present at Manití/Vainilla but absent from the other sites.

Excluding allospecies, a total of 25 species recorded at Manití/Vainilla were absent from both Tambopata and Manu (Table 1). Approximately 130 species, recorded at Tambopata appear to be absent from Manití/Vainilla. Of these, half are restricted to *varzea* forest. A total of 105 species recorded at Manu are apparently absent at Manití/Vainilla. Of these, about half are restricted to *varzea* forest. As mentioned above, virtually the entire forest surveyed at Manatí/Vainilla was *terra firme*. This comparison supports Remsen and Parker's (1983) assertion of the importance of river-created habitats in contributing to overall avian diversity in the Amazon Basin.

We cannot explain the apparent absence of some *terra firme* species that are known from both the Tambopata and Manu sites. Specifically, the following Tambopata/Manu species missing from the Manití/Vainilla sites are found on the nearby north bank of the Amazon

Table 1. Species present at Manití/Vainilla, but not at the Tambopata and/or Manu sites. An 'X' indicates that a species was missing. An asterisk (*) indicates that the species is replaced by an allospecies at the other two sites. Thus, if allospecies are taken into account a total of 25 species are absent from both the Tambopata and Manu sites.

	Tambopata	Manu		Tambopata	Manu
Milvago chimachima		X	*Hypocnemis hypoxantha*	X	X
Pyrrhura picta	X		*Percnostola schistacea*	X	X
Neomorphus pucheranii *	X	X	*Myrmeciza melanoceps* *	X	X
Chlorostilbon mellisugus	X	X	*Myrmeciza fortis*	X	
Amazilia fimbriata	X	X	*Hylophylax naevia*	X	
Pharomachrus pavoninus		X	*Phlegopsis erythroptera*	X	X
Trogon rufus	X	X	*Conopophaga aurita* *	X	X
Bucco tamatia	X	X	*Liosceles thoracicus*	X	
Bucco capensis	X		*Lophotriccus vitiosus*	X	X
Galbula dea		X	*Cnipodectes subbruneus*	X	X
Malacoptila rufa *	X	X	*Myiobius barbatus*	X	
Nonnula rubecula	X	X	*Myiobius atricaudus*	X	X
Capito aurovirens	X	X	*Attila citriniventris*	X	X
Piculus flavigula	X	X	*Conopias parva*	X	X
Denconychura stictolaema	X	X	*Machaeropterus regulus*	X	X
Xiphorhynchus ocellatus	X		*Manacus manacus*	X	X
Sclerurus rufigularis	X	X	*Chiroxiphia pareola*	X	X
Frederickena unduligera	X		*Pipra pipra*	X	X
Thamnophilus murinus	X	X	*Pipra filicauda* *	X	X
Neoctantes niger	X		*Psarocolius viridis*	X	X
Thamnomanes saturninus *	X	X	*Cacicus haemorrhous*		X
Myrmotherula obscura	X	X	*Cyanerpes nitidus*	X	X
Myrmotherula haematonota *	X	X	*Tachyphonus surinamus*	X	X

(LSUMNS unpubl. data): *Momotus momota*, *Philydor erythropterus*, *Myrmotherula hauxwelli*, *Formicarius analis*, *Pachyramphus minor* and *Habia rubra*. Two other species apparently do not range this far north in Peru: *Myrmotherula leucophthalma* and *Pipra chloromeros*.

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APPENDIX

List of 328 species recorded at the combined Manití/Vainilla site, with estimated relative abundance and general habitat preferences. Species marked with an asterisk (*) were collected. Trinomials are given where positive subspecies determinations could be made.

Coding for abundance symbols:

- C common, recorded (seen or heard) daily in fairly large numbers (>10 individuals)
- F fairly common, recorded daily in smaller numbers (< 10 individuals)
- U uncommon, recorded most days, but always in smaller numbers
- R rare, not recorded daily, usually seen on one of every five or six days, always in small numbers
- X one record only, status uncertain

General habitat preferences:

1. Primary *terra firme* forest
2. Clearings, secondary forest and other man-made habitats
3. River edge

Species	Abundance	Habitat
T. major	U	1
T. guttatus *	F	1
Crypturellus cinereus	U	1
C. soui nigricans *	F	2,3,1
C. undulatus	U	3,2
C. bartletti *	R	1
C. variegatus *	F	1
Zebrilus undulatus *	X	1
Sarcoramphus papa	R	1
Coragyps atratus	U	2,1
Cathartes aura	U	2,1
C. melambrotos	C	1
Elanoides forficatus	R	1
Leptodon cayanensis	U	1
Harpagus bidentatus bidentatus *	U	1
Ictinia plumbea	U	1
Rostrhamus hamatus	X	1
Buteo magnirostris *	R	2,1
B. brachyurus	X	1
Leucopternis kuhli *	U	1
L. schistacea *	U	1
Morphnus guianensis *	X	1
Harpia harpyja	X	1
Herpetotheres cachinnans *	U	1
Micrastur mirandollei *	R	1
M. gilvicollis *	U	1
Daptrius ater	U	1
D. americanus *	U	1
Milvago chimachima	U	3,2
Falco rufigularis	X	1
Penelope jacquacu	X	1
Odontophorus stellatus	R	1
Laterallus fasciatus	U	2
Columba plumbea delicata *	F	1
Columbina talpacoti	U	3,2
Leptotila rufaxilla *	U	3,2
Geotrygon montana montana *	F	1
Ara ararauna	U	3,1
A. manilata	R	1
Aratinga weddellii *	U	3,2
Pyrrhura picta luciani *	C	2,1
Forpus xanthopterygius	U	1,2
Brotogeris cyanoptera cyanoptera *	C	1,3
Pionites leucogaster xanthomeria *	F	1,2
Pionopsitta barrabandi	U	1
Pionus menstruus	R	1
Amazona amazonica	U	1
A. farinosa *	C	1
Coccyzus melacoryphus	X	2
Piaya cayana *	F	1,2
P. melanogaster *	U	1,2
P. minuta	F	2
Crotophaga major	U	3,2
C. ani *	C	2
Tapera naevia	R	2
Neomorphus pucheranii *	X	1
Otus choliba	U	1
O. watsonii *	F	1
Lophostrix cristata	U	1
Pulsatrix perspicillata	U	1
Glaucidium brasilianum	U	1,2
Ciccaba virgata *	R	1
Nyctibius griseus	R	1,2
Lurocalis semitorquatus	X	1

Nyctidromus albicollis albicollis *	C	2
Chaetura sp.	C	2
C. brachyura *	C	2
Tachornis squamata *	C	2
Glaucis hirsuta affinis *	F	1
Threnetes leucurus cervinicauda *	U	1
*Phaethornis superciliosus ochraceiventris**	R	1
P. hispidus *	R	1
P. philippii *	F	1
Florisuga mellivora *	C	1,2
Anthracothorax nigricollis nigricollis *	R	2,1
Popelairia langsdorfii	R	1
Chlorostilbon mellisugus *	X	2
Thalurania furcata viridipectus *	U	1
Chrysuronia oenone josephinae *	U	1,2
Amazilia fimbriata *	U	2,3
Polyplancta aurescens *	U	1
Pharomachrus pavoninus *	F	1
Trogon melanurus melanurus *	U	1
T. viridis *	F	1
T. collaris	R	1
T. rufus sulphurens *	U	1
T. violaceus	F	1
Ceryle torquata	R	3
Chloroceryle amazona	U	3
Chloroceryle aenea aenea *	R	3
Electron platyrhynchum	R	1
Baryphthengus martii *	R	1
Galbula cyanicollis *	U	1
G. dea *	U	1
Jacamerops aurea isidori *	R	1
Notharchus macrorhynchus hyperrynchus *	R	1
Bucco macrodactylus *	U	1,2
B. tamatia pulmentum *	R	1
B. capensis *	U	1
Malacoptila rufa rufa *	U	1
Nonnula rubecula cineracea *	U	1
Monasa nigrifrons nigrifrons *	F	1
M. morphoeus peruana *	C	1
Capito aurovirens *	R	3,2
C. niger *	F	1
Pteroglossus castanotis	U	1,2
P. flavirostris mariae *	R	1,2
P. beauharnaesii *	U	1
Selenidera reinwardtii	F	1
Ramphastos culminatus	F	1
R. cuvierii	F	1
Picumnus borbae juruanus *	R	2
Piculus flavigula flavigula *	U	1
Celeus elegans	F	2
C. grammicus grammicus *	R	1
Dryocopus lineatus	U	1
Melanerpes cruentatus	F	2
Veniliornis affinis hilaris *	U	1
Campephilus melanoleucos	U	1
C. rubricollis trachelopyrus *	U	1
Dendrocincla fuliginosa phaeochroa *	F	1
D. merula bartletti *	U	1
Deconychura longicauda connectens *	X	1
D. stictolaema secunda *	U	1
Sittasomus griseicapillus	X	1
Glyphorhynchus spirurus castelnaudii *	C	1
Nasica longirostris *	R	3,2
Dendrexetastes rufigula	U	3
Dendrocolaptes certhia juruanus *	R	1
Xiphorhynchus picus peruvianus *	F	3,2
X. obsoletus palliatus *	R	1
X. ocellatus *	R	1
X. spixii juruanus *	C	1
X. guttatus guttatoides *	U	1
Lepidocolaptes albolineatus	R	1,2
Cranioleuca gutturata *	U	1
Hyloctistes subulatus subulatus *	U	1
Ancistrops strigilatus	U	1
Philydor erythrocercus subfulvus *	R	1
P. pyrrhodes *	R	1
Automolus ochrolaemus ochrolaemus *	R	1
A. rufipileatus	X	1
A. infuscatus infuscatus *	U	1
Xenops milleri *	U	1
X. tenuirostris *	R	1
X. minutus obsoletus *	U	1
Sclerurus rufigularis *	R	1
S. caudacutus brunneus *	U	1
Cymbilaemus lineatus intermedius *	F	1
Frederickena unduligera *	R	1
Taraba major melanurus *	U	2
Thamnophilus doliatus	U	2,3
T. aethiops kapouni *	R	1
T. schistaceus	R	1
T. murinus canipennis *	F	1
Pygiptila stellaris maculipennis *	U	1
Neoctantes niger *	R	1
Thamnomanes saturninus huallagae *	C	1
T. caesius/schistogynus *	R	1
Myrmotherula sclateri *	U	1
Myrmotherula brachyura brachyura *	F	1
M. obscura *	R	1
M. surinamensis	R	2,3
M. haematonota haematonota *	U	1
M. axillaris melaena *	F	1
M. longipennis *	R	1
M. menetriesii menetriesii *	U	1
Dichrozona cincta *	U	1
Terenura humeralis *	U	1

Cercomacra cinerascens	C	1
C. nigrescens	R	1,3
C. serva hypomelaena *	C	1
Myrmoborus myotherinus elegans *	R	1
Hypocnemis cantator peruviana *	U	2
H. hypoxantha hypoxantha *	F	1
Percnostola schistacea *	F	1
P. leucostigma subplumbea *	R	1
Sclateria naevia argentata *	R	1
Myrmeciza hemimelaena hemimelaena *	C	1
M. melanoceps *	R	1
M. fortis fortis *	U	1
M. atrothorax obscurata *	C	2,1
Gymnopithys salvini maculata *	F	1
Rhegmatorhina melanosticta purusiana *	U	1
Hylophylax naevia theresae *	F	1
H. poecilonota gutturalis *	F	1
Phlegopsis erythroptera ustulata *	R	1
Chamaeza nobilis nobilis *	R	1
Formicarius colma nigrifrons *	R	1
Myrmothera campanisona minor *	R	1
Conopophaga aurita australis *	R	1
Liosceles thoracicus erithacus *	U	1
Zimmerius gracilipes gracilipes *	U	1,2
Ornithion inerme *	R	1
Camptostoma obsoletum	U	2
Phaeomyias murina wagae *	U	2
Tyrannulus elatus *	C	2,1
Myiopagis gaimardii guianensis *	F	2,1
M. caniceps cinerea *	R	2
Elaenia parvirostris *	U	2
Mionectes oleagineus hauxwelli *	F	1
Leptopogon amaurocephalus peruvianus *	U	1
Corythopis torquata sarayacuensis *	F	1
Myiornis ecaudatus ecaudatus *	F	1
Lophotriccus vitiosus congener *	F	1
Todirostrum latirostre caniceps *	U	2
T. chrysocrotaphum *	U	1
Cnipodectes subbruneus minor *	U	1
Ramphotrigon ruficauda *	R	1
Rhynchocyclus olivaceus aequinoctialis *	U	1
Tolmomyias assimilis clarus *	F	1
T. poliocephalus *	F	1
T. flaviventris viridiceps *	U	2
Platyrinchus coronatus coronatus *	U	1
P. platyrhynchos senex *	X	1
Onychorhynchus coronatus castelnaui *	U	1
Terenotriccus erythrurus brunneifrons *	F	1
Myiobius barbatus amazonicus *	F	1
Myiobius atricaudus adjacens *	X	1
Cnemotriccus fuscatus	U	3
Pyrocephalus rubinus	R	2
Attila citriniventris *	F	1
Attila cinnamomeus *	R	1
Attila spadiceus spadiceus *	R	1
Rhytipterna simplex *	U	1
Laniocera hypopyrrha *	U	1
Myiarchus tuberculifer tuberculifer *	X	2
Myiarchus swainsoni *	R	1
Myiarchus ferox ferox *	F	2
Pitangus sulphuratus sulphuratus *	R	2,1
Megarhynchus pitangua pitangua *	U	2,1
Myiozetetes similis	C	2,1
M. granadensis	U	2,1
M. luteiventris luteiventris *	U	1
Conopias parva *	F	1
Myiodynastes maculatus solitarius *	F	1
Legatus leucophaius leucophaius *	U	2
Empidonomus varius	R	1
*E. a. aurantioatrocristatus**	U	1
Tyrannus melancholicus melancholicus *	C	2
Pachyramphus castaneus saturatus *	U	2,1
P. polychopterus tenebrosus *	U	2,3
P. marginatus	F	1,2
Tityra cayana	U	1
Schiffornis major major *	U	3,2
S. turdinus amazonus *	F	2
Piprites chloris tschudi *	F	1
Tyranneutes stolzmanni *	F	1
Machaeropterus regulus striolatus *	U	1
Manacus manacus interior *	U	2
Chiroxiphia pareola regina *	R	1
Pipra pipra *	C	1
P. coronata coronata *	F	1
P. filicauda filicauda *	U	1,2
P. rubrocapilla *	U	1
Iodopleura isabellae	R	1
Lipaugus vociferans	C	1
Cotinga maynana *	U	1,2
C. cayana cayana *	F	1,2
Gymnoderus foetidus	U	1
Querula purpurata	R	1
Tachycineta albiventer	U	3
Progne chalybea	U	3
P. elegans	X	3
Atticora fasciata	C	3
Stelgidopteryx ruficollis ruficollis *	C	3
Cyanocorax violaceus	R	1
Thryothorus leucotis	F	3
Troglodytes aedon	C	2
Microcerculus marginatus marginatus *	F	1
Cyphorhinus arada salvini *	R	1,2
Turdus ignobilis	F	2
T. lawrencii	R	1

T. hauxwelli *	R	2
T. albicollis spodiolaemus *	U	1
Ramphocaenus melanurus amazonum *	U	1
Vireolanius leucotis simplex *	U	1
Vireo olivaceus solimoensis *	U	1,2
Hylophilus thoracicus aemulus *	R	1
H. hypoxanthus fuscicapillus *	C	1
H. ochraceiceps ferrugineifrons *	U	1
Molothrus bonariensis *	U	2
Scaphidura oryzivora	U	2,1
Clypicterus oseryi	U	1
Psarocolius viridis	R	1
P. angustifrons angustifrons *	C	2,1
Gymnostinops yurucares	R	1
Cacicus cela cela *	C	2,3
C. haemorrhous	U	1
C. solitarius	R	3,2
Icterus cayanensis *	U	2
Cyanerpes nitidus	F	1,2
C. caeruleus microrhynchus *	C	1,2
C. cyaneus	U	1,2
Chlorophanes spiza caerulescens *	C	1,2
Dacnis cayana glaucogularis *	U	1,2
D. lineata lineata *	F	1,2
D. flaviventer *	F	2
Euphonia xanthogaster dilutior *	U	1,2
E. minuta minuta *	R	1,2
E. laniirostris melanura *	R	1,2
E. rufiventris *	F	1,2
Tangara velia iridina *	U	1,2
T. callophrys *	F	1,2
T. chilensis chilensis *	C	1,2
T. schrankii schrankii *	F	1
T. xanthogastra xanthogastra *	U	1
T. mexicana boliviana *	U	1,2
T. gyrola	R	1
Thraupis episcopus	C	2
T. palmarum melanoptera *	C	2
Ramphocelus carbo carbo *	C	2
R. nigrogularis	C	2,3
Lanio versicolor versicolor *	F	1
Tachyphonus surinamus napensis *	F	1
T. rufiventer *	U	1
Eucometis penicillata	U	1
Hemithraupis flavicollis peruana *	F	1,2
Lamprospiza melanoleuca	U	1
Cissopis leveriana leveriana *	U	2
Saltator maximus maximus *	U	2
S. coerulescens	C	2
Pitylus grossus	R	1
Cyanocompsa cyanoides rothschildii *	U	1
Sporophila americana murallae *	R	2
S. castaneiventris	C	2
Oryzoborus angolensis torridus *	U	2
Ammodramus aurifrons	R	2,3

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Contributions of Charles S. Boyer (1856-1928) to the Knowledge of Diatoms (Bacillariophyceae): Biographical Notes, Literature and Taxonomic Summary, with Type Designations

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ABSTRACT.—Biographical notes on Charles Sumner Boyer (1856- 1928), prominent U.S. diatomist and member of The Academy of Natural Sciences, are presented along with a listing of his publications spanning the period 1891-1927. The names of 77 new taxa and 104 new combinations published by him are included, as well as 4 additional new taxa attributed to others (*Achnanthes linearis* fo. *curta* H. L. Smith *ex* Boyer, *Pleurosigma olympianum* W. A. Terry *ex* Boyer, *Surirella americana* W. A. Terry *ex* Boyer, and *Surirella woolmaniana* C. L. Peticolas *ex* Boyer). Types are designated for taxa described as new in his publications, including 41 holotypes, 36 lectotypes, and 43 isotypes. Four previously designated types (3 lectotypes and 1 neotype) are also included. [Bacillariophyceae, Boyer bibliography, C. S. Boyer, diatoms, types]

Although short articles have been written about the well-known U.S. diatomist Charles Sumner Boyer, neither his publications nor his taxonomic contributions to the study of diatoms have been summarized in the literature. This report is intended to correct those deficiencies and to give a brief account of some events in his life.

Born of German and French parentage in Philadelphia on September 24, 1856, Boyer was educated in the public school system graduating from Central High School in 1874. He continued his education at Brown University, Providence, R. I., receiving the baccalaureate degree in 1879 (with the honor of being class poet) and the Master of Arts degree in 1885. His first formal instruction in botany was as a member of W. W. Bailey's class at Brown University.

Before that, at the age of about eight, he had already become interested in the microscope and is quoted by Booth [*in* The Observer, section on Practical Microscopy, July, 1895, p. 108] as saying: "I can scarcely remember when I did not possess some kind of a microscope . . . . My passion for microscopy has become so much a part of my life, that I would rather part with anything almost than give up my instrument."

After graduation, Boyer returned from

Providence, R. I. to Philadelphia and began teaching mathematics, Latin and Greek in private schools. He then entered the public school system as principal of the Nebinger School and then of the Northwest School. In 1891 he became Supervising Principal of the newly built William D. Kelley School.

While teaching in Philadelphia, Boyer became associated with the Academy of Natural Sciences (ANSP), publishing his first paper on diatoms in 1891 at the age of 35. The next year Edward Woolman and Benjamin Sharp nominated him for membership in the Academy and on February 23, 1892, he was accepted as a full member.

Considerable time was spent at the Academy working with Mr. John A. Shulze and other volunteers making slide mounts and cataloging various collections at hand, most importantly the Christian Febiger Collection, the earliest and largest world-wide collection of diatoms in the United States. The Febiger collection formed the nucleus of the present Diatom Herbarium.

In addition to his membership at the Academy of Natural Sciences, Boyer became a member of the American Microscopical Society, Torrey Botanical Club, Geographical Club, American Academy of Political and Social Sciences and was a Fellow of the Royal Microscopical Society.

According to available records, Charles Boyer and Ella Harriet Talbot were married in Providence, Rhode Island in 1880 and had three children: Edith (b.1882 - d.1949), Carl (b.1884 - d.1955) and Harriet (b.1886 - d.1954). After the death of his wife in 1911, he was married for a second time in 1920 to Amanda Jane Rogers, a teacher at the William D. Kelley School (Huebner 1990). Boyer died in Philadelphia on March 28, 1928, in his 72nd year.

Not much was found concerning Boyer's activities during the early 1900's except as contained in a few remarks about his work, included in the following section on his publications.

Parts of the above information were gleaned from the Academy Archives, Anonymous (1895) and Harshberger (1899).

PUBLICATIONS

Boyer's earlier publications reflect his development and direction in the study of diatoms. In his first paper on etymology, he registered surprise and delight on the descriptive nature of Latin and Greek-derivative generic names applied by earlier workers. In this paper, he made use of the word "diatomaniac", probably the first (and perhaps only) public record of this jest, still in current usage.

The 1891 paper was followed by articles on diatom "cleaning" and mounting techniques, interposed by a paper on the movement of *Bacillaria paradoxa* Gmel. filaments. Around 1894-1895, his attention seemed to focus on the subject of fossil diatoms. This was probably due not only to his association with Shulze and Keeley (ANSP), but also to his association with geologist Lewis Woolman who began supplying him with fossil material from artesian wells in the area.

Interest in fossil diatoms seems to have continued throughout his career, but his initial enthusiasm for living diatoms, both fresh water and marine, was by no means overridden. He was constantly collecting diatoms from all sorts of habitats in and around Philadelphia. This took him on many excursions, i.e. to New Jersey (he had a "laboratory" in Ancora, New Jersey) and to the Media-area (Delaware and Chester counties, Pennsylvania) where he and his colleague Dr. T. Chalkley Palmer collected extensively. Both men were associated both with the Academy of Natural Sciences and with the Delaware County Institute of Science in Media.

These years of excursion and experience culminated in the publication (1916) of a book "The Diatoms of Philadelphia and Vicinity" in which Boyer accounted for 530 diatom taxa (fresh water, marine, fossil and living) including approximately 700 illustrations. Letters and requests from all parts of the world indicate

that this publication was extremely well received. The illustrations accompanying the descriptions were particularly applauded.

Over half of the diatom taxa published by Boyer as new appeared in several papers published between 1920-1926, just prior to his last and most comprehensive publication, "Synopsis of the North American Diatomaceae." The synopsis still remains the only compilation summarizing taxa of fresh, brackish and marine diatoms from North America. About 2,000 taxa were described; no illustrations were included. A complete list of Boyer's publications is given in Appendix 1.

TAXA PROPOSED IN BOYER'S HONOR

Four diatom species have been named in his honor: *Pyxidicula boyeri* Pantocsek (1909), *Pleurosigma boyeri* Keeley (1925), *Neidium boyeri* Reimer (1959), and *Pinnularia boyeri* Patrick (1966). A new generic name ("*Boyeria*") was proposed by G. Dallas Hanna in 1928. The following circumstances occasioned it:

In the first part of The Synopsis of the North American Diatomaceae (1927a, p. 89) Boyer noted that the diatom species *Eupodiscus radiatus* Bailey might have to be placed in a new genus and suggested that it be called "*Baileya*".

On March 7, 1928, Hanna wrote a letter to Boyer pointing out that the name *Baileya* had previously been used for a higher plant. [It had also previously been applied as a diatom generic name by Marsson (1901).] Hanna then wrote, "If it is agreeable to you, I would like to propose *Boyeria* for the group but will not do so if you have already prepared to treat of it or if you have any objections to your name being so used." Whether Boyer responded to this letter is unknown (Boyer died three weeks later). Apparently the generic name "*Boyeria*" has never been used.

TAXA DESCRIBED AS NEW IN THE PUBLICATIONS OF C. S. BOYER (WITH TYPE DESIGNATIONS)

In Appendix 2, all taxa described as new by Boyer are listed and types are designated. This includes the names of four taxa attributed to Peticolas (1), Terry (2) and H. L. Smith (1), which appeared in his papers.

All holotypes designated here are to be attributed to Boyer, this in conformance with Article 7(7.3) of the International Code of Botanical Nomenclature (ICBN) (Greuter et al. 1988).

Boyer left careful notes with slide numbers, localities and Maltwood Finder coordinates for most of his new taxa. In some cases he wrote "type" and/or "N.Sp." on the slide, on the draft plate legend, or in his handwritten log book.

All but three of the Holotype designations are single mounts and the specimen on the designated slide corresponds in detail with his published photomicrographs. Holotype specimens for *Pinnularia asburyana*, *Glyphodesmis campechiana* and *Stauroneis frickei* var. *angusta*, which were illustrated with line-drawings, were marked by Boyer with Maltwood Finder coordinates. In all cases they agree with details of the description and illustration.

The authors of this paper are responsible for designations of lectotypes, neotypes, and isotypes, when not otherwise indicated.

NEW COMBINATIONS MADE BY C. S. BOYER

Scattered throughout the publications of C. S. Boyer are diatom names considered as new combinations (Appendix 3). In all but his latest works, only the author(s) of the basionym was given in parenthesis after the specific or varietal epithet followed by a citation for the basionym; for example:

"*Biddulphia Californica* (A. S.)
Ceratulus Californica A. S., Schmidt, Pl. 115, figs 2, 3, 4"

In his last publications he added his own name to the combination; for example:

"*Caloneis speciosa* (Hustedt) Boyer
Navicula speciosa Hust. *in* A. Schmidt, Atlas pl. 295"

These combinations satisfy the requirements called for in Art. 32.3 & 32.4 (ICBN). To have completed a literature search establishing the actual legitimacy of each combination would have gone beyond the scope of this paper. Therefore we have indicated Boyer's combinations as later homonyms only in such cases where our available search time revealed an earlier homonym.

Boyer's new combinations, in alphabetical order, are presented in Appendix 3.

THE C. S. BOYER DIATOM COLLECTION

In 1957, the Academy received about 1,000 diatom collections (bottles & bags) from the widow of Cyrus Chappell, a diatomist friend of Boyer. During our recent program of backlog-curating, we discovered among this material a whole series of Boyer's diatom samples long considered permanently lost. We can only assume that Chappell had these samples on loan from Boyer. In any event, these additions brought the Material Collection of Boyer to a total of 1,503 samples of "loose" material.

There are 5,266 Boyer slides in the collection. Both slide and material collections remain housed as an entity, except for a few of his slides previously accessioned in the General Collection and the Shulze Collection. All information in Boyer's original card catalog has been duplicated in the Herbarium's Taxon and Locality Files which are currently being integrated into a computer database.

Slides, bottle and bag material, notebooks, and the personal Maltwood Finder and microscope of Boyer are available in the Diatom Herbarium (ANSP). Although it is highly desirable to examine slides in the herbarium proper, loan of an individual type could be effected if conditions warrant. Small aliquots of most loose material are also available for research purposes. In accordance with our loan policy, a loan can be made only through an institution and not directly to an individual.

POST SCRIPTUM

Diatom research in the United States has spanned a period of approximately 150 years, essentially launched by J. W. Bailey, a professor at West Point Military Academy, New York (Edgar 1978). This was just about 50 years after diatoms began to be recognized as a distinct group of microorganisms (Gmelin 1788, Kützing 1844).

From this beginning, there developed geographical foci where interest in diatoms was centered (i.e. Boston-New England Area, Philadelphia Area, Washington Area, Lower Great Lakes-Midwest Area, California-West Coast Area). This development was also closely associated with the founding of numerous microscopical clubs and societies throughout the country. For a more detailed history of diatom studies in the U. S., see Patrick (1984).

Certainly, Philadelphia was one of the earliest centers of diatom study in the U. S. and of all the mid-19th to early 20th century diatomists associated with the Philadelphia-group, Boyer must be considered the most significant figure. He not only amassed the largest personal (reference) collection of diatom slides and material (over 6,000 samples), he was also the most prolific publisher of his research work at the Academy during that period (Appendix 1).

He certainly was *not* one of those often derided amateurs who were merely *delighted* with "slides of diatom skeletons, so elegantly disposed" (Lewin 1962). Actually, much of the early research work published on diatoms was based on the discoveries and technical advances of these enthusiastic and innovative "amateurs."

We believe that Boyer did his research (all on his own time and without remuneration) in the best tradition of a dedicated scientist driven by the challenge of those tiny one-celled plants living in "glass houses."

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APPENDIX 1

Publications of Charles S. Boyer

1891 Diatoms and Etymology. The Microscope 11:207-208.

1893 The cleaning of Diatomaceous material. I & II. The Observer 4:171-175, 207-209.

1894 *Bacillaria paradoxa*. Microscopical Bulletin & Science News 11:43-44.

1895a A Diatomaceous deposit from an Artesian Well at Wildwood, N. J. Bulletin of the Torrey Botanical Club 22:260-266.

1895b A fossil marine Diatomaceous deposit at St. Augustine, Florida. Bulletin of the Torrey Botanical Club 22:171-174.

1895c Marine and fresh-water diatoms from a unique bed between the depths of 78 and 181 feet, at Wildwood, N. J., as identified by C.S. Boyer. Geological Survey of New Jersey; Annual Report of the State Geologist for the year 1894. Trenton, N. J.:163-165, plate 6.

1895d The mounting of diatoms. I & II. Practical Microscopy 6:6-7, 70-73.

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1899a New species of diatoms. Proceedings of the Academy of Natural Sciences of Philadelphia for 1898, vol. 50:468-470, pl. 24.

1899b Notes on diatoms. *In*: Woolman, L.; Fossil mollusks and diatoms from the Dismal Swamp, Virginia and North Carolina; indications of the geological age of the deposit. Proceedings of the Academy of Natural Sciences of Philadelphia for 1898, vol. 50:414-428.

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1909 A new species of *Cymatopleura*. Proceedings of the Academy of Natural Sciences of Philadelphia for 1908, vol. 60:554, pl. 28.

1911 Jelly-pores in the Diatomaceae. Proceedings of the Academy of Natural Sciences of Philadelphia for 1910, vol. 62:271.

1914 A new diatom. Proceedings of the Academy of Natural Sciences of Philadelphia, vol. 66:219-221, pl. 10.

1916 The Diatomaceae of Philadelphia and vicinity. J. P. Lippincott Company, Philadelphia, Pennsylvania: 143 pp., pls. 1-40.

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1926 List of Quaternary and Tertiary Diatomaceae from deposits of southern Canada. Canada Department of Mines, Victoria Memorial Museum, Museum Bulletin 45, Biological Series No.12:1-26.

1927a Synopsis of the North American Diatomaceae. Part I. Coscinodiscatae, Rhizosolenatae, Biddulphiatae, Fragi-

lariatae. Proceedings of the Academy of Natural Sciences of Philadelphia for 1926, 78 supplement:3-228.

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1927c A list of Diatomaceae. *In*: Howe, M. A.; Report on a collection of marine algae made in Hudson Bay. Report of the Canadian Arctic Expedition 1913-1918, Vol. 4, Part B, Botany:26-28.

Publications of Boyer, C. S. and F. J. Keeley

1907 Notes on diatoms. *In*: Arnold, R. & R. Anderson; Geology and oil resources of the Santa Maria Oil District, Santa Barbara County, California. United States Geological Survey Bulletin 322:40-41, pls. 19-20.

APPENDIX 2

Taxa described as new in the publications of C. S. Boyer (with type designations)

When the type designation is preceded by a single asterisk, an individual specimen is meant, whether as a single mount, or as a specimen singled out in a strewn mount by coordinates. In the latter case, the specimen has been ringed with a diamond scribe. Two asterisks preceding the type designation indicate an illustrated specimen. When three asterisks precede a type designation, an entire population on a permanent slide mount is indicated. The absence of an asterisk preceding the listed type indicates a previous designation.

Achnanthes linearis f. *curta* H. L. Sm. *ex* Boyer, 1916, p. 59, pl. 16, fig. 16,17.
*LECTOTYPE = Boyer A-2-21
specimen coord.: **MF 26**
9
***ISOTYPE = Boyer A-5-4

Actinocyclus ellipticus var. *delawarensis* Boyer, 1916, p. 27, pl. 3, fig. 6.
*LECTOTYPE = Boyer 375
specimen coord.: **MF 26**
26

Actinoptychus trilineatus Boyer, 1922, p. 1, pl. 1, fig. 1.
**LECTOTYPE = Boyer, 1922, pl. 1, fig. 1.

Actinoptychus vulgaris var. *interrupta* Boyer, 1916, p. 24, pl. 4, fig. 5.
*LECTOTYPE = Boyer 658
specimen coord.: **MF 24**
10
***ISOTYPE = Boyer 376

Amphora pavimentum Boyer, 1922, p. 1, pl. 1, fig. 4.
**LECTOTYPE = Boyer, 1922, pl. 1, fig. 4.

Anaulus priscus Boyer, 1922, p. 2, pl. 1, fig. 3.
*HOLOTYPE = Boyer F-7-2 (single mount)

Anomoeoneis serians var. *apiculata* Boyer, 1927b, p. 325; Lewis, 1865, pl. 2, fig. 5a.
NEOTYPE = Boyer 392 (*design*: Reimer, 1961)

Auliscus floridanus Boyer, 1920c, p. 67, pl. 2, fig. 3.
**LECTOTYPE = Boyer, 1920, pl. 2, fig. 3

Auliscus hyalinus Boyer, 1920c, p. 67, pl. 2, fig.4.
*LECTOTYPE = Boyer 237
specimen coord.: **MF 22**
12

Auliscus shulzei Boyer, 1922 p. 2, pl. IV, fig. 1.
*LECTOTYPE = Shulze A 1253 (single mount)
*ISOTYPE = Boyer O-4-5 (single mount)

Biddulphia arctica var. *pentagona* Boyer, 1901, p. 715.
*LECTOTYPE = Boyer B-4-18 (single mount)

Biddulphia arctica var. *sexangulata* Boyer, 1901, p. 715.
*LECTOTYPE = Boyer C-4-1 (single mount)

Biddulphia argus Boyer, 1899a, p. 469, pl. XXIV, fig. 6.
*LECTOTYPE = Boyer X-4-13
specimen coord.: **MF 18**
30

Biddulphia centralis Boyer, 1922, p. 2, pl. III, fig. 3.
*HOLOTYPE = Boyer P-6-3 (single mount)

Biddulphia clypeolus Boyer, 1922, p. 2, pl. III, fig. 1.
*HOLOTYPE = Boyer R-6-15 (single mount)
*ISOTYPE = Boyer J-7-14 (single mount)

Biddulphia costata Boyer, 1922, p. 2, pl. II, fig. 8.
*HOLOTYPE = Boyer P-7-3 (single mount)

Biddulphia curvinervia Boyer, 1922, p. 3, pl. III, fig. 11.
*HOLOTYPE = Shulze A-3461 (single mount)

Biddulphia falcata Boyer, 1922, p. 3, pl. III, fig. 4.
*HOLOTYPE = Boyer E-6-21 (single mount)

Biddulphia fulva Boyer, 1922, p. 3, pl. III, fig. 2.
*HOLOTYPE = Boyer J-6-17 (single mount)

Biddulphia hexagonalis Boyer, 1922, p. 3, pl. III, fig. 5.
*HOLOTYPE = Shulze A-3458 (single mount)

Biddulphia immanis Boyer, 1922, p. 3, pl. II, fig. 2.
*HOLOTYPE = Boyer O-6-11 (single mount)
*ISOTYPE = Boyer T-6-24 (single mount)

Biddulphia inflata var. *recta* Boyer, 1922, p. 4, pl. I, fig. 7.
*HOLOTYPE = Shulze A 3460 (single mount)

Biddulphia interrupta Boyer, 1899a, p. 468, pl. XXIV, fig. 2.
*LECTOTYPE = Boyer R-2-20 (single mount)

Biddulphia keeleyi Boyer, 1899a, p. 469, pl. XXIV, fig. 4.
*HOLOTYPE = Boyer Y-2-7 (single mount)

Biddulphia nervata Boyer, 1922, p. 4, pl. II, fig. 1.
*HOLOTYPE = Boyer X-6-10 (single mount)
*ISOTYPE = Boyer X-6-9 (single mount)

Biddulphia quadrans Boyer, 1922, p. 4, pl. 1, fig. 5.
*HOLOTYPE = Shulze A 3459 (single mount)

Biddulphia semicircularis var. *asburyana* Boyer, 1901, p. 726 [Boyer 1899a, p. 469, pl. 24, fig. 3]
*LECTOTYPE = Boyer N-4-14 (single mount)
*ISOTYPE = Boyer X-3-25
specimen coord: **MF 29**
23

Biddulphia shulzei Boyer, 1899a, p. 470, pl. XXIV, fig. 7,8.
*HOLOTYPE = Shulze A 1667 (single mount)

Biddulphia spicata Boyer, 1922, p. 4, pl. II, fig. 3.
*HOLOTYPE = Boyer P-7-8 (single mount)

Biddulphia subquadrata Boyer, 1922, pp. 4-5, pl. I, fig. 8.
*HOLOTYPE = Boyer P-6-7 (single mount)
*ISOTYPE = Boyer P-6-14 (single mount)
*ISOTYPE = Boyer P-6-24 (single mount)

Biddulphia verrucosa Boyer, 1899a, p. 468, pl. XXIV, fig. 5.
*LECTOTYPE = Boyer X-3-22 (single mount)

Brebissonia palmerii Boyer, 1916, p. 80, pl. 17, fig. 8.
*LECTOTYPE = Boyer 591
specimen coord.: **MF 25**
13

Brightwellia hillabyana Boyer, 1922 p. 5, pl. I, fig. 2.
*HOLOTYPE = Boyer P-7-2 (single mount)

Caloneis barbadensis Boyer, 1922 p. 5, pl. I, fig. 6.
*HOLOTYPE = Boyer P-7-4 (single mount)

Caloneis permagna var. *lewisiana* Boyer, 1916, p. 82, pl. 21, fig.2.
*LECTOTYPE = Boyer 273
specimen coord.: **MF 28 28**
33 34

Chaetoceros elmorei Boyer, 1914, pp. 219-220, pl. X, fig. 1-7.
***LECTOTYPE = Boyer X-5-14
***ISOTYPE = Boyer C-1-2
***ISOTYPE = G.C. 8436
***ISOTYPE = G.C. 8437

Coscinodiscus incompositus Boyer, 1922, p. 5, pl. II, fig. 6.
*HOLOTYPE = Boyer P-6-17 (single mount)

Coscinodiscus jeremianus Boyer, 1922, p. 5, pl. IV, fig. 2.
*HOLOTYPE = Boyer E-6-13 (single mount)
*ISOTYPE = Boyer S-5-2 (single mount)

Coscinodiscus lewisianus var. *hillabyanus* Boyer, 1922, pp. 5-6, pl. II, fig. 7
*HOLOTYPE = Boyer P-7-5 (single mount)
*ISOTYPE = Boyer Y-6-12 (single mount)
*ISOTYPE = Boyer Y-6-13 (single mount)
*ISOTYPE = Boyer Z-6-19 (single mount)
*ISOTYPE = G.C. 15439 (single mount)

Cymatopleura elliptica f. *spiralis* Boyer, 1916, p. 129, pl. 37, fig. 2.
*HOLOTYPE = Boyer E-2-14 (single mount)

Cymatopleura shulzei Boyer, 1909, p. 554, pl. XXVIII, fig. 1-3.
*HOLOTYPE = Shulze A-3369 (single mount)

Cymbella heteropleura var. *symmetrica* Boyer, 1927b, p. 278.
*LECTOTYPE = Boyer 835
specimen coord.: **MF 33**
23

Cymbella philadelphica Boyer, 1916, p. 63, pl. 18, fig. 8.
*LECTOTYPE = Boyer 658
specimen coord.: **MF 14**
13

Cymbella rhomboidea Boyer, 1916, p. 63, pl. 18, fig. 11.
*LECTOTYPE = Boyer 772
specimen coord.: **MF 19**
20

Dictyoneis marginata var. *maxima* Boyer, 1916, p. 79, pl. 20, fig. 1.
*HOLOTYPE = Boyer V-2-17 (single mount)

Dimerogramma intermedium Boyer, 1920c, p. 67, pl. 2, fig. 11.
*LECTOTYPE = Boyer 883
specimen coord.: **MF 20**
15

Diploneis excentrica Boyer, 1916, pp. 85-86, pl. 20, fig. 10.
*LECTOTYPE = Boyer 292
specimen coord.: **MF 39**
26
***ISOTYPE = Boyer 191
***ISOTYPE = Boyer 225

Entogonia confusa Boyer, 1922, p. 6, pl. III, fig. 8.
*HOLOTYPE = Boyer A-7-8 (single mount)

Entogonia furcata Boyer, 1922, p. 6, pl. III, fig. 6.
*HOLOTYPE = Boyer P-7-9 (single mount)

Entogonia occlusa Boyer, 1922, p. 6, pl. III, fig. 10.
*HOLOTYPE = Boyer I-6-5 (single mount)

Entogonia porrecta Boyer, 1922, p. 6, pl. III, fig. 9.
*HOLOTYPE = Boyer D-7-24 (single mount)

Entogonia subrostrata Boyer, 1922, p. 7, pl. III, fig. 7.
*HOLOTYPE = Boyer P-7-7 (single mount)

Eunotia stevensonii Boyer, 1920c, p. 69, pl. 2, fig. 12. fig. 13?
*LECTOTYPE = Boyer 778
specimen coord.: **MF 25**
22

Glyphodesmis campechiana Boyer, 1920c, p. 68, pl. 2, fig. 10.
*HOLOTYPE = Boyer 894
specimen coord.: **MF 16**
24

Glyphodesmis tumida Boyer, 1920c, p. 68, pl. 2, fig. 2.
*HOLOTYPE = Boyer 865
specimen coord.: **MF 21**
37

Hydrosera nova-caesareae Boyer, 1895a, p. 263.
*LECTOTYPE = Boyer R-3-19
specimen coord.: **MF 22**
25
***ISOTYPE = Boyer 330
***ISOTYPE = Boyer 331

Navicula brasiliensis (*bicuneata*) f. *constricta* Boyer, 1916, p. 92, pl. 25, fig. 2.
**HOLOTYPE = Boyer, 1916, pl. 25, fig. 2

Navicula hasta var. *punctata* Boyer, 1916, p. 97, pl. 27, fig. 14.
**HOLOTYPE = Boyer, 1916, pl. 27, fig. 14.

Navicula mobiliensis Boyer, 1922, p. 8, pl. II, fig. 5.
*LECTOTYPE = Boyer 747
specimen coord.: **MF 30**
23
***ISOTYPE = Boyer 1041
***ISOTYPE = G.C. 2955

Navicula pusilla var. *subcapitata* Boyer, 1916, p. 91, pl. 25, fig. 8.
*LECTOTYPE = Boyer 591
specimen coord.: **MF 30**
28

Nitzschia semicostata Boyer, 1920c, p. 70, pl. 2, fig. 6.
**HOLOTYPE = Boyer, 1920, pl. 2, fig. 6.

Opephora pinnata var. *lanceolata* Boyer, 1916, p. 44 pl. 10, fig. 17.
*LECTOTYPE = Boyer 272
specimen coord.: **MF 27**
25

Pinnularia asburyana Boyer, 1922, p. 8, pl. IV, fig. 5.
*HOLOTYPE = Boyer 610
specimen coord.: **MF 20**
20

Pinnularia blandita Boyer, 1916, p. 108, pl. 30, fig. 25.
*LECTOTYPE = Boyer 376
specimen coord.: **MF 30**
19

Pinnularia hagelsteinii Boyer, 1920c, p. 69, pl. 2, fig. 7.
*LECTOTYPE = Boyer 980
specimen coord.: **MF 26**
28
***ISOTYPE = G.C. 60858

Pinnularia major var. *pulchella* Boyer, 1916, p. 102-103, pl. 28, fig. 2.
LECTOTYPE = Boyer 426 (*design*: Patrick, 1966)
*ISOTYPE = BOYER F-7-5 (single mount)
***ISOTYPE = Boyer N-2-15

Pinnularia viridis var. *caudata* Boyer, 1916, p. 104, pl. 30, fig. 18.
LECTOTYPE = Boyer V-5-2 (*design*: Patrick, 1966)

Pleurosigma olympianum Terry *ex* Boyer, 1927b, p. 470.
*LECTOTYPE = Boyer X-5-7
specimen coord.: **MF 20**
14

Rattrayella recens Boyer, 1922, p. 8, pl. III, fig. 6.
*HOLOTYPE = Boyer 1041
specimen coord.: **MF 29**
26

Rhabdonema woolmanianum Boyer, 1899a, p. 468, pl. XXIV, fig. I, 1a, 1b.
*LECTOTYPE = Boyer X-3-16
specimen coord.: **MF 27 27**
22 23
***ISOTYPE = Boyer Y-3-2
***ISOTYPE = G.C. 43020
***ISOTYPE = G.C. 43022
*ISOTYPE = Shulze A 512 (single mount)
*ISOTYPE = Shulze A 513 (single mount)
*ISOTYPE = Shulze A 514 (single mount)
***ISOTYPE = Shulze A 1039
***ISOTYPE = Shulze A 1525
***ISOTYPE = Shulze A 1526

Stauroneis frickei var. *angusta* Boyer, 1916, p. 88, pl. 26, fig. 18.
*HOLOTYPE = Boyer V-5-3
specimen coord.: **MF 12**
17

Stephanodiscus gayhartianus Boyer, 1922, p. 8, pl. IV, fig. 7.
*HOLOTYPE = Boyer A-4-6 (single mount)

Stictodiscus convexus Boyer, 1922, p. 9, pl. IV, fig. 4.
*HOLOTYPE = Boyer D-7-25 (single mount)

Surirella americana Terry *ex* Boyer, 1927b, p. 543.
*LECTOTYPE = Boyer X-5-6
specimen coord.: **MF 24**
24

Surirella palmerii Boyer, 1920c, p. 70, pl. 2, fig. 14, 15.
*LECTOTYPE = Boyer C-6-1
specimen coord.: **MF 19**
20

Surirella woolmaniana Peticolas *ex* Boyer, 1895a, p. 265.
*LECTOTYPE = G.C. 3121
specimen coord.: **MF 21**
31

Synedra anguinea Boyer, 1920c, p. 68, pl. 2, fig. 1.
*LECTOTYPE = Boyer 31
specimen coord.: **MF 25**
19

Synedra incisa Boyer, 1920c, p. 68-69, pl. 2, fig. 8.
LECTOTYPE = Boyer A-6-5 (*design*: Patrick, 1966)

Synedra pulchella var. *flexella* Boyer, 1916, p. 49, pl. 12, fig. 2.
*LECTOTYPE = Boyer Q-5-19
specimen coord.: **MF 9**
20

Syringidium poyserii Boyer, 1922, p. 9, pl. II, fig. 4.
*HOLOTYPE = Boyer G-7-8 (single mount)
*ISOTYPE = Boyer J-7-16 (single mount)
*ISOTYPE = Boyer K-7-4 (single mount)
*ISOTYPE = Boyer L-7-10 (single mount)
*ISOTYPE = Boyer L-7-13 (single mount)
*ISOTYPE = Boyer P-7-6 (single mount)
*ISOTYPE = G.C. 2593 (single mount)
*ISOTYPE = G.C. 15065 (single mount)
*ISOTYPE = G.C. 15393 (single mount)

Trachyneis barbadensis Boyer, 1922, p. 9, pl. 4, fig. 3.
*HOLOTYPE = Boyer P-7-1 (single mount)

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Contributions of Henry Weed Fowler (1878-1965), with a Brief Early History of Ichthyology at The Academy of Natural Sciences of Philadelphia

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ABSTRACT.—Biographical notes on Henry Weed Fowler (1878-1965), prominent American ichthyologist and first Curator of the fish collection of the Academy of Natural Sciences of Philadelphia, are presented with emphasis on his contributions to the development of ichthyology at that institution. Brief accounts are also given of selected ichthyologists of the last century and their association with the Academy of Natural Sciences of Philadelphia.

Publication of the *Journal of the Academy of Natural Sciences of Philadelphia* begun in 1817, provided a ready forum for many of the leading American ichthyologists of the nineteenth century (the U.S. Government did not begin issuing its own publications until after 1878) and stimulated interest in the study of fishes at the Academy. As the reputation of the institution grew, many fishes were added to the Academy's collection but there was comparatively little activity either in identification of specimens or research on them until 1897 when Henry Weed Fowler (23 March 1878 - 21 June 1965) was given responsibility for the curation of "cold-blooded" vertebrates at the Academy. Although a brief biography (M. Phillips 1964) and obituary (Conant 1966) of Fowler are available, his dedication to ichthyology has never been fully appreciated and many aspects of his life and long association with the Academy have never been summarized or adequately documented.

In February, 1893 the Board of Curators of the Academy of Natural Sciences received a carefully hand-written letter from a precocious fifteen year old from Holmsburg, Pennsylvania. "Gentlemen," it began,

> Having determined to devote my life to the study of Natural History, I respectfully apply for a studentship at the Academy of Natural Sciences.
>
> I have for five years studied the structure and anatomy of birds, having had no other teacher excepting the few books given to me or that I bought, or those I had access to by the kind permission of the librarian of the Academy of Natural Sciences.
>
> With this I have studied drawing or ornithological drawing, making many sketches of birds, many of them from the Academy's museum.

Fig. 1. Henry Weed Fowler (1878-1965), circa 1949.

> I can draw many species of English and American birds from memory. I am familiar with the higher order of birds, comprising the vultures, eagles, falcons, and hawks.
>
> I went to the Columbia School (grammar school) where I stood very high in history, geography and drawing. I can refer you to Mr. Swift my teacher as to my ability to study Natural History, and also my character while at school. Hoping this will receive your consideration, I remain
>
> Yours truly
>
> Henry Fowler[1]

Except for a two year stint, beginning in 1901, as a special student of David Starr Jordan at Stanford University, this self-educated ornithologist turned ichthyologist would personify the Fish Department at the Academy of Natural Sciences for almost three quarters of a century.[2] Henry Weed Fowler not only authored 666 publications[3] totaling more than 19,000 pages of text, the majority profusely illustrated by the author, he also amassed at the Academy one of the most important and best documented ichthyological collections in the world (for a complete bibliography see Phillips and Phillips 1965; Böhlke 1984a).

Fowler's involvement with the Academy's fish collection was a result of his very early and strong interest in both art and natural history, traits that characterized his entire career. The circumstances that led to Fowler's introduction to the Academy have been described (M. Phillips 1964:128 [4]) as follows:

> As a boy he became absorbed in learning to draw and paint. This interest led him, when he was fifteen, to construct a large mural painting which extended around two sides of his room. It was made on a huge sheet of wrapping paper measuring six by twenty feet. It depicted a scene on the Orinoco River, his interest having been aroused by a book on the natural history of that part of South America. He visited the Academy of Natural Sciences of Philadelphia to examine specimens of plant and animal life of that region, so that he might paint the proper fish in the stream, birds in the air, and trees and flowers on the bank. What he saw at the Academy so intrigued him that in 1894, through the encouragement of Samuel G. Dixon, later president of the Academy, he became associated with the institution as a Jessup student.[4]

At an early age Fowler began to keep detailed records of his field trips.[5] His entries frequently record observations on life colors, relative abundance, preferred habitats and spawning behavior of the fishes he and others encountered. His large personal collection of fishes, a product of these early investigations, was soon donated to the Academy.

Fowler's interest in fishes rapidly extended beyond the fauna of his immediate vicinity. His first two ichthyological papers (Fowler 1899a, 1899b), concerned fishes from such disparate localities as Jamaica and China, respectively, and established his life-long habit of publishing on collections of fishes from around the globe as they were received. For better or worse, Fowler will probably be most remembered as the last ichthyologist who attempted to revise

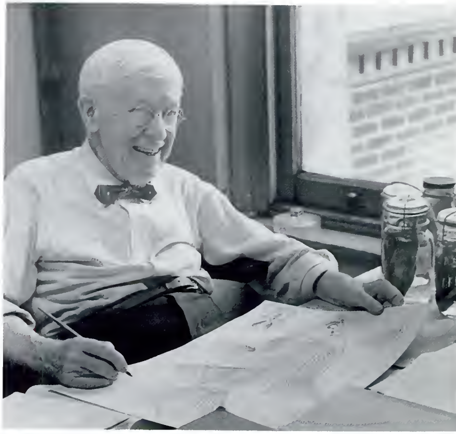

Fig. 2. Henry Weed Fowler, circa 1958, still very active at 80 years.

singlehandedly the taxonomy of the fishes of the world.

Looking through Fowler's publications is like scanning an international gazetteer, for his papers discuss fishes from Altoona to Zanzibar. A random sampling of titles include descriptions of fishes of Australia, Belize, Bolivia, Brazil, Ceylon, Chile, China, Cuba, Ecuador, Fiji, Guam, Haiti, Jamaica, Java, Madagascar, Malaya, New Zealand, Panama, Peru, the Philippines, Siam, South Africa, Sumatra, Tahiti, and Viet Nam. Nor did his interest stop with fish. Birds (his first love), crustacea, reptiles, and amphibians also captured his attention and worked their way into his busy research and publication schedule. His greatest single contribution to the field of herpetology was his "Amphibians and reptiles of New Jersey" (Fowler 1907a).

In his early days Fowler made frequent collecting trips to New Jersey, Delaware, Maryland and throughout much of Pennsylvania. On vacations and week-ends he often went to "the shore," especially Cape May, N.J. to meet the incoming fishing boats. In his quest for new and rare specimens, he haunted fish markets and became a familiar figure to both sport and commercial fisherman.

Fowler also traveled more widely — to the southern United States, the Florida Keys, Hawaii, China, and the South Pacific — but many, if not most, of the fishes he studied were collected on his behalf by others. By all accounts, Fowler was a genius at acquiring specimens. He rewarded his collectors with prompt and thorough publications on their contributions, often honoring them in the process with patronyms, thereby encouraging still more collecting. Fowler's bibliography virtually constitutes a list of Academy acquisitions throughout the first half of the twentieth century, with the history of each major collection routinely recorded in the introduction of his papers [for a brief summary of major acquisitions of historical interest, see Böhlke (1984a)].

The following excerpts from a selection of Fowler's letters illustrate his zeal for acquiring specimens for the museum:[6]

20 March 1934 to Otway H. Brown

I am delighted with the specimens you sent . . . . The two small fish are extra-ordinary! The long slender one is a Bellows fish or Snipe Fish (*Macrorhamphosus*). The deep bodied fish, rosy colored, is a Boar fish, belonging to the family Antigoniidae. Both are new species! They will be named for Mr. Otter and yourself. I am at work preparing the necessary drawings and descriptions and hope to have them finished this week so that they can be placed with our Publication Department. When the papers are printed, I shall be glad to send both you and Mr. Otter copies . . . . Having made such an excellent beginning, I hope both Mr. Otter and yourself will keep the eternal vigilance on those fish boats because I am sure you cannot fail to happen on still further rarities and novelties.

12 April 1934 to Otway H. Brown

I cannot urge too strongly that you pick up any small odd looking fish, as you see we know very little about the fishes off shore. There are many species which you may happen on at any time and I will be delighted to work them up. It will take me a short time yet before I have a chance to get at these fishes, but will eventually get the accounts into print.

29 December 1936 to Vernon E. Brock

I would be very much interested in the collection of fishes from your region which you outline. We have very few Pacific fishes from your region, and they are just a few duplicates which the United States Fish Commission sent us many years ago. A collection of moderate or small specimens, such as you have in mind, would be most welcome; and I shall be glad to try and help you in every way possible, either with literature or attempts at identification, if you so desire.

29 March 1937 to Director of Agriculture [Fiji Islands]

At the present time Mr. George Vanderbilt of New York, U.S.A. is cruising through various groups of Polynesian Islands in the eastern Pacific and collecting materials for our museum . . . . What we need most would be extensive collections of all of the smaller fishes from as many different islands, also as many different localities as possible from each of those islands, besides details of native names along with trustworthy observations, so that we may first be able to work out their distribution. As to the details of collecting, I am enclosing a sheet we use for our field work,[7] also a series of diagrams pertaining to large, unwieldy specimens, so that we may have such details preserved and forwarded to us along with photographs and in that way reconstruct such of the picture as may be available.

24 January 1938 to Vasco Bensaude

I wish to thank you for this little collection and hope you might be induced to arrange to get us some more materials from there [Sao Tome]. I should especially like a collection of 50 to 100 specimens, or more, both marine and fresh water . . . . If you would arrange to secure the collection I have suggested, I shall be very glad to exchange papers on ichthyology which I have published. As these are quite extensive and run into many pages with numerous figures, I should like to have a comparatively extensive collection of fishes in return . . .

27 March 1938 to Joseph Bequaert

Knowing you have had an opportunity to visit the Congo region, I trust if you should go there again you will kindly arrange to secure fresh water fishes and allow me to work them over.

28 August 1939 to Dr. Carlos Moralles Macedo

Through my friend, Mr. W. Stephen Thomas, who has recently been in Peru and having met you, I learn that you may possibly be interested in some kind of arrangement for the exchange of Peruvian fishes with the Academy. We have some fine old collections made in your country

by Professor James Orton many years ago. . . . I have on hand a large Peruvian collection received several years ago, and am now engaged in finishing the manuscript report [see Fowler 1940a]. . . . It occurred to me that possibly you may be willing to exchange Peruvian fishes with us for publications.

27 September 1940 to Professor P.W. Fattig

Through my friend, Dr. Francis Harper, I have learned that you may be induced to secure fishes from Georgia for us, and ask if you would care to undertake making up some local collections from the different water-courses. Knowing you are interested in natural history, and perhaps more in herpetology, I could offer you in exchange papers of general nature or dealing with North American Herpetology.

25 November 1943 from Captain Edward L. Jackson

I am, of course, very glad to learn that some of these fishes that I sent you are new . . . . As to letting you know where these fishes come from — that is absolutely impossible, because of the military situation. It was only with some difficulty that I got permission to send you the fishes at all, and in order to get that permission, I had to assure the Base Censor that you would not be able to tell, by examining the fishes, where they had come from. I could not under any circumstances identify the locality for you, and I know that any attempt on your part, back in the states, to learn what this A P O (Army Post Office) number stands for, would result in my being ordered not to send you any further specimens, and might result in disciplinary action being taken, in addition. I am sorry that this is the case, and assure you that the moment the censorship regulations permit it, I will give you the information.[8]

Fowler's collectors were legion, including virtually anyone he could entice to send or save him specimens, but his most famous collaborator was not an ichthyologist at all. During the summer of 1934, Fowler spent six weeks with Ernest Hemingway aboard the writer's boat, *Pilar*, plying the waters off Cuba for Marlin, Sailfish, Dolphin, and Shark.[9]

While the company may have been more memorable than the catch, Fowler appreciated his host's efforts enough to describe a new species, *Neomerinthe hemingwayi*, in his honor (Fowler 1935a). The information and specimens Hemingway provided the Academy from subsequent fishing excursions enabled Fowler to refine the scientific knowledge of many of the important North Atlantic game fishes. Hemingway had a passion for fishing (especially for marlin) and his interest in furthering research on all aspects of billfishes was serious enough that in one of his *Esquire* articles (Hemingway 1934), he posed a number of interesting questions about their biology, offered some of his own explanations, and lamented the lack of adequate scientific subsidies. His own generous assistance to Fowler and the Academy notwithstanding, Hemingway concluded that ". . . you cannot expect anyone to subsidize anything that anybody has a swell time [doing]."

In addition to acquiring specimens via donations from others and as a result of his personal collecting efforts, Fowler added to the collection by arranging exchanges of duplicates with other institutions. One such exchange was with the United States National Museum, in which the Academy was to receive the third set of specimens of Philippine fishes obtained by the U. S. Bureau of Fisheries Steamer "Albatross" 1907-1910 from all the groups involved in Fowler's studies.10 Fowler was employed as a consultant by the Smithsonian Institution in 1925 to describe the fishes from this enormous collection in its entirety. He had intended to treat on a family-by-family basis all of the Albatross fishes, and the bulk of this work was published in seven volumes, totaling 2,982 pages, of Bulletin 100 of the U. S. National Museum (Fowler and Bean 1928, 1929, 1930; Fowler 1931b, 1933, 1941a, 1943). However, much of Fowler's labor devoted to this task was reported (Hubbs 1964:58) to have "resulted

only in filling cabinets full of unpublished manuscripts."[11]

When the young Henry Fowler first arrived at the Academy, the institution had been in existence for over eighty years, and was generally recognized as one of the preeminent scientific institutions in the world. Although there had been no paid caretaker or curator of fishes for the first 85 years of its history, from 1812 to 1897, there had been considerable interest in ichthyology at the Academy almost from the first day of the institution's founding in 1812.[12] Most of the important early students of ichthyology in eastern North America were either resident or corresponding members of the Academy, sharing their knowledge, if not always their specimens, with fellow members of the Academy.[13]

Alexander Wilson (1766-1813) and Samuel Latham Mitchill (1764-1831) were two such members. Although Wilson is far better known for his pioneering work in American ornithology, he did name and describe two of the regions's most abundant and important fishes — the alewife (*Alosa pseudoharengus*) and the American shad (*Alosa sapidissima*) — before his untimely death less than a year after the Academy's founding. Samuel Mitchill, a New York naturalist who was described by one of his contemporaries as "a living encyclopedia," published one paper in the Academy's *Journal* (Mitchill 1818), but is best known for his pioneering works on the fishes of New York (1814-15).[14]

Records do not indicate whether either gentleman deposited any of their specimens at the Academy. If so, their identity and provenance have unfortunately been lost; as Fowler (1945:4) explained, many of the Academy's earliest specimens were "marked with outside labels, written in ink and tied about the neck of the jar by a strong cord. As the cases were often damp and with poor light, many of the labels molded or became illegible." In August 1899, unusually heavy rains and a broken water main caused the Academy's basement to fill with more than five feet of water, further damaging the external labels on many of the fish specimens that were stored there.[15]

Perhaps the most active of the Academy's earliest ichthyologists was Charles Alexandre LeSueur (1778-1846), a French naturalist whose artistic abilities earned him as wide a reputation as his knowledge of American fish. When LeSueur arrived in Philadelphia in 1817, he had already established a reputation for artistic talent and scientific excellence during a four-year survey of Australian natural history sponsored by Napoleon Bonaparte, and a six month collecting trip in the Caribbean organized and financed by the Academy's president, William Maclure (1763-1840).[16] Lesueur was elected to membership - and a curatorial post - in the Academy immediately after his arrival in Philadelphia.[17] He published 20 papers on fishes in the Academy's *Journal*, including that publication's first ichthyological paper (LeSueur 1817).

LeSueur left Philadelphia with several other Academy members in 1825 to help establish a utopian community in New Harmony, Indiana. There he served as a surveyor, architect, physician, teacher, businessman, and portraitist. He returned to France in 1837 to help found and direct the museum of natural history at Le Havre. Three fish specimens collected by LeSueur are still identifiable in the Academy's collections (two syntypes of *Cyprinus maxillingua* and the holotype of *Acipenser brevirostrum*).[18]

Another Frenchman whose efforts brought luster and specimens to the Academy was Charles Lucien Bonaparte (1803-1857), nephew of the Emperor Napoleon. He was elected to Academy membership in 1824, and published several ornithological papers in the Academy's *Journal*. Approximately 2,000 Bonaparte specimens comprising nearly 500 species (as listed in the original collection catalogue, dated 1849) are still owned by the Academy.[19] Primarily fishes from Italy and the Mediterranean, they formed the basis for Bonaparte's three volume *Fauna Italica* (1832-1841) and also the *Catalogue of the Fresh Water Fishes of Europe* (1846). Included in the collection are the types of about nominal 40 species.

Constantine Samuel Rafinesque (1783-1840), the most eccentric and controversial of the Academy's early members, published only one ichthyological paper (Rafinesque 1818) in the Academy's *Journal* [see Hanley (1977) and Boewe (1982) for more biographical information about Rafinesque]. Unfortunately, none of Rafinesque's fish specimens are extant.[20] As Call (1899) has noted, Rafinesque did not preserve any type material.

Some of the first fishes to catch Henry Fowler's eye at the Academy were in a collection from Samoa and the Sandwich Islands [Hawaii] (Fowler 1900) secured by the ornithologist John Kirk Townsend (1808-1851) and the botanist Thomas Nuttall (1786-1859) at the end of their historic trans-continental collecting expedition of 1835.[21] About 100 species are represented by the 200 surviving specimens from this collection. Although exceeded in number and importance by collections made during the U.S. Exploring Expedition (1838-1842) under the command of Captain Charles Wilkes (1798-1877), the Townsend-Nuttall specimens represent the oldest fishes from Oceania in any North American institution.

John Edwards Holbrook (1794-1871), known for his pioneering work in American herpetology and the fishes of his native South Carolina, contributed a number of specimens to the Academy's collection, and an important paper on the fishes of Florida and Georgia to the Academy's *Journal* (Holbrook 1855).

Although Theodore Nicholas Gill (1837-1914) donated few specimens to the collection, he published 163 titles in the *Proceedings*, between 1860 and 1878 during his residency in Philadelphia, and before he went to the Smithsonian Institution. Fowler (1945:18) considered his catalog of East Coast fishes (Gill 1862), published as a separate volume by the Academy, to be "of the greatest importance for the various checklists following down to our time."

While several historically important collections of Academy fishes were purchased, the great majority were donated or obtained during expeditions sponsored by members and friends of the institution. Two of the most important expedition sponsors were Rodolphe M. de Schauensee (Fowler 1931a, 1934a, 1934c, 1935b, 1936a, 1937, 1939) and George Vanderbilt (Fowler 1936c, 1940b, 1941b, 1944a).

Fig. 3. Edward Drinker Cope (1840-1897).

Of all the famous Philadelphia naturalists associated with the Academy, it was Edward Drinker Cope (1840-1897) who amassed the largest and most important collections prior to the arrival of Henry Fowler.[22] In 1859, about the time Cope had decided to forsake a career in agriculture that his father had wished him to pursue, he began his association with the Academy by recataloging, without remuneration, the entire herpetological collection (Maline 1978:91). A pioneer in the development of American vertebrate paleontology, and one of the most dominant and controversial personalities of his era, Cope is not usually remembered for his ichthyological contributions (see Osborn 1931 for biography and complete bibliography). However, Cope published the descriptions of 424 nominal species of fish (of which the Academy has types of 341). Cope's will

specified that all his collections preserved as wet preparations were to be given to the Academy of Natural Sciences (Osborn 1931:453). Happily, Fowler had an opportunity to meet Cope before taking charge of his collection. Although he had seen him in and about the Academy, it was a visit to Cope's Pine Street home in 1894 that left the most lasting impression on the young ichthyologist:[23]

> Jacob Geismar was employed by Cope as an assistant or helper and after opening the door, told me to follow. Great slabs of rock with fossils were banked around in the hallway and rooms and in the offing of what appeared to have been the parlor and dining room were two badly mounted caribou. We ascended the stairway and walked back to the sitting room, where Geismar left me with Cope. ... The table he was sitting before was small, and it was piled high with all kinds of books, papers and various specimens. ... All about the floor were numbers of old-fashioned screw-topped pale green preserve jars filled with reptiles and fishes in alcohol. Large ones of several gallons in content were parked about nearer the walls or in protected places. They appeared very formidable, as each had a large sheet of foolscap or other white paper pasted on the outside, each containing long columns of scientific names. No other clues to the contents appeared. At that time, I little thought that several years later, the task would fall to me to transport all of this material to the Academy.

After questioning Fowler about his interest in natural history, Cope treated the young man to one of his famous discourses on the topic while puffing away on a large cigar. "I shall never forget the cordiality of Cope that day and of having the opportunity of a most entertaining time in talking to him about his collections," recalled Fowler. "I saw and conversed with him many times later, [but] my first meeting was the only real lesson in natural history he ever gave me."

Fowler oversaw the transfer of Cope's entire alcoholic collection to the museum in 1898 and spent the next several years trying to decipher Cope's cryptic notes and organize the collection. As noted by Böhlke (1984a:6), "after writing somewhat critically of Cope's treatment of specimens, Fowler adopted almost identical practices in his later years," as when he packed assorted collections of poorly labeled specimens into large jars and crocks.

Inspired by the challenge of accessioning this material, Fowler vowed to personally illustrate not only all the species in Cope's collection that had not previously been illustrated, but every unfigured species in the rest of the Academy's collection as well. He never fully completed this task, but the manuscript collection of the Academy contains the original published illustrations of over 4,000 species, plus some 2,300 additional Fowler drawings that are unpublished. During a conversation with the late James E. Böhlke, Fowler explained that he read and wrote during his long train commute to and from the Academy, and that he outlined penciled illustrations at work and inked them at home in the evening, always giving each fish "a little individuality," from memory if not from the specimen (Böhlke 1984a:6). Some of the most interesting of Fowler's illustrations (Fig. 4) are 283 unpublished drawings[24] (218 inked, 64 in pencil, one half-inked) of a large collection of fish skeletons prepared by Dr. Carl Joseph Hyrtl (1810-1894) of Vienna in the early 1800's and purchased by Cope during a visit to Europe in the 1870's.[25] Fowler had intended to use them as illustrations for his ambitious *Catalog of World Fishes*, (see below) only part of which was published.

Fowler's abilities as an illustrator, like everything else in his career, came from his own desire and self-instruction. Early in his career he did receive some criticism from David Starr Jordan. In a 1901 letter, Jordan offered to allow Fowler to come to Stanford University as a graduate student without charges with the possibility of paying for his room and board by working as an illustrator. He then went on to offer these comments on Fowler's work:

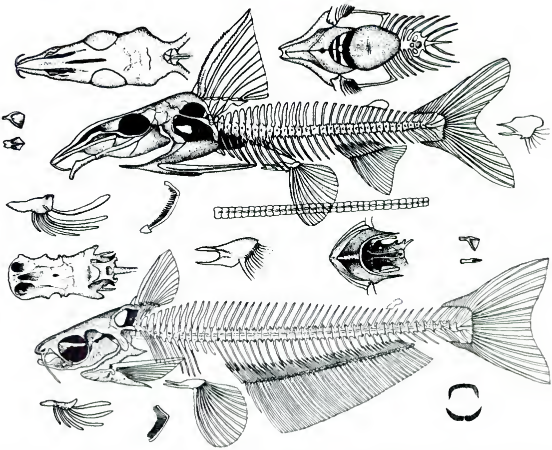

Fig. 4. Two of Fowler's unpublished illustrations of Hyrtl fish skeletons in the Archives of the Academy of Natural Sciences: above, *Doras carinatus* (Linneaus); below *Auchenipterus nuchalis* (Spix).

> I have looked over carefully the drawings which you have published. They are accurate enough but they lack certain fine touches in detail and they seem to be extremely rough in grade. Perhaps this roughness is not the fault of the artist. We have here Mrs. Starks [Chloe Leslie Starks], perhaps the finest fish artist that has yet developed in this country, who, I have no doubt, would give you some coaching so as to make your work acceptable, especially on the easier fishes and those that do not need to be magnified. If you want to take your chances, there are about 200 species here to be drawn, and the Smithsonian pays fifty cents a square inch, multiplying the greatest length by the greatest depth. The drawings are usually made large and then reduced.[26]

Such advice, and years of practice, honed Fowler's skills to considerable advantage. Given the circumstances and rapidity in which his drawings were made, the results are remarkably good (Fig 5).

During his 63+ years of active ichthyological research,[27] Fowler had an unprecedented opportunity to study many new collections of fishes from around the world, and, if he could not find a previous description that closely matched a specimen in hand, he did not hesitate to coin a new scientific name for it. Fowler described some 1,404 new species of Recent fishes (not counting substitute names), of which the Academy has primary types [holotypes, lectotypes or syntypes] of 1,013 nominal species. Given the difficulity of examining type specimens at other institutions during most of his era and, *especially*, the rate and breath of Fowler's publications, it is not surprising that many of his new taxa have proved to be invalid.[28]

One circumstance that compromised specimen comparisons even at his own institution was the lack of an adequate supply of glass jars. As Fowler's reputation grew and more and ever-larger collections of fishes were sent for

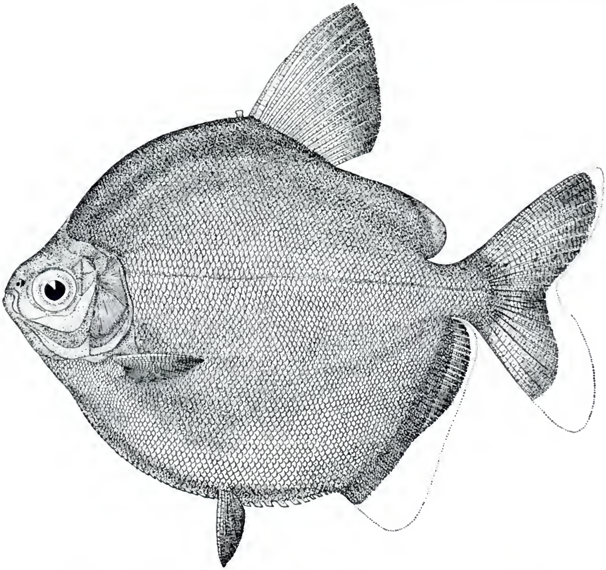

Fig. 5. Drawing of lectotype (ANSP 8024) of *Myletes lippincottianus* Cope; from Fowler (1907b, fig. 57).

identification, this problem intensified. It was Fowlers' usual habit to study (and almost simultaneously write a manuscript on) each collection of fishes in the order that it was received. To conserve space, individual collections were wrapped together with cheesecloth and tied in small bundles; these were then tightly packed in large crocks, each filled to capacity and sealed, making it virtually impossible to locate and re-examine previously studied material.

What sets Fowler apart from most of his contemporaries was his willingness to undertake large regional monographs, usually without the assistance of coauthors. In addition to major reports on the Albatross Phillipine fishes, de Schauensee and George Vanderbilt expeditions cited previously, Fowler produced lengthy works on the *Fishes of Oceania* (1928, 1931c, 1934b, 1949), *Marine Fishes of West Africa* (1936b, 1936d), *Fishes of the southern piedmont and coastal plain* (1945), *Fishes of the Red Sea and southern Arabia* (1956) and *Fishes of Fiji* (1959). Other large undertakings of many years duration were his *Synopsis of the fishes of China*, (1930-1962), which appeared in three different journals in 36 parts totaling 1,377 pages [see Phillips and Phillips (1965) for complete listing], his *Os Peixes de Agua do Brasil* (1948-1954), and his monumental final work *Catalog of World Fishes* (see below). A summary of Fowler's bibliography by journal and subject categories (Table 1) illustrates why his name will be familiar to any serious student

of fish taxonomy.

Fowler's *Catalog of World Fishes* was partially published in 27 parts by the Taiwan Museum in their Quarterly Journal (1964-1967), nearly 2,000 printed pages [see Böhlke (1984b) for complete listing].[29] As Conant (1966) so accurately predicted, Fowler "... was a cataloger in a broad sense, and his works will long serve as the foundation" on which future ichthyologists can build their monographs and detailed studies. Eschmeyer (1990) in the introduction to his *Catalog of the Genera of Recent Fishes* gives a detailed account of the history and circumstances surrounding the continued publication of this series more than a decade after Fowler's death, remarking that "probably the most useful source in preparing the Catalog was Henry W. Fowler's *Fishes of the World*." He also stated that Fowler's Catalog (including unpublished parts) contained some generic names and earlier publication references that otherwise might have been over-looked; these enabled him to find errors in his own database that had gone undetected.

Although Fowler was one of the founders of the American Society of Ichthyologists and Herpetologists and later briefly served as the society's president (1927-1928), he was far more interested in the substance of his work than in the politics of professional organizations. He kept his administrative duties at the Academy to a minimum in order to devote more time to his research and publications. Fowler was known as an engaging raconteur on a wide range of subjects - from his early days at the Academy, to his fishing experiences with Ernest Hemingway. One friend remembered his small office at the Academy as being "piled so high with bottles of specimens, stacks of literature, drawings, fish skeletons, and other objects" that he seemed completely isolated from the rest of the world. Perhaps it was Fowler's self-imposed isolation that enabled him to produce so much. Whatever his secret, he was totally dedicated to the study of fishes and left behind a lifetime of achievement that has seldom been equaled.

CHRONOLOGY

1878	Born March 23, Holmesburg, Pennsylvania [now section of Philadelphia] son of Joel C. Fowler and Helen Weed Fowler
188?	Attended Emmanuel Parish School & Columbia Consolidated School [both at Holmesburg]
1894	Jessup student, Academy of Natural Sciences [ANSP]
1899	First paper published on fishes [see Fowler (1899a)]
1901-02	Special student, Leland Stanford University
1902	Assistant Curator of "cold-blooded" vertebrates, ANSP
1904	Member of Clarence B. Moore Florida Expedition [Fowler's first major expedition - Florida Keys.]
1909	Married to Elizabeth Keim (1884-1970)
1922	Awarded Bishop Fellowship in Yale University [which enabled him to travel to Hawaii to begin work that culminated in his "Fishes of Oceania"]
1925	Birth of only child, Henry W. Fowler, Jr.
1925-	Consultant to Smithsonian Institution, commissioned to prepare reports on "Albatross" Philippine Collections
1927-28	President of American Society of Ichthyologists and Herpetologists
1928-	Consulting Ichthyologist, Bernice P. Bishop Museum
1929	Traveled to Hawaii, Japan, China, Java and Australia
1934	Collected gamefish with Ernest Hemingway in Cuba
1944-45	Worked on Hyrtl skeleton collection at University of Pennsylvania
1949	Traveled to Caribbean coast of Colombia [Grant from American Philosophical Society]
1965	Died 21 June, Newtown, Bucks County, Pennsyvania

Table 1. Summary of Henry Weed Fowler publications by subject categories. Codes = **A**, Recent fishes; **B**, Fossil fishes & archaeological; **C**, Nomenclature of fishes; **D**, Popular articles on fishes; **E**, Amphibians & reptiles; **F**, Combination of A + E; **G**, Birds; **H**, Invertebrates; **I**, Other

Dates	Sources	Codes								
		A	B	C	D	E	F	G	H	I
1897-1906	The Auk	-	-	-	-	-	-	3	-	-
1899-1952	Proceedings of the Academy of Natural Sciences of Philadelphia	137	-	-	-	4	3	1	-	-
1901-1916	Cassinia	-	-	-	-	-	-	6	-	-
1902-1941	Proceedings of the United States National Museum	22	-	-	-	-	-	-	-	-
1903-1915	Science (n.s.)	12	-	3	-	-	-	-	-	1
1904	Journal of the Academy of Natural Sciences of Philadelphia	1	-	-	-	-	-	-	-	-
1904-1940	Proceedings of the American Philosophical Society	2	-	-	-	-	-	-	-	-
1906-1912	Annual Report of New Jersey State Museum	2	-	-	-	1	2	-	1	-
1906	Forest and Stream	1	-	-	-	-	-	-	-	-
1906-1916	American Naturalist	5	-	-	-	1	-	-	-	-
1907	Star and Wave [Cape May, NJ newspaper]	-	-	-	1	-	-	-	-	-
1908	Bucks County Gazette [Bucks County, PA newspaper]	-	-	-	1	-	-	-	-	-
1911	Geological Survey of New Jersey Bulletin	-	1	-	-	-	-	-	-	-
1913-1963	Copeia	47	-	5	-	12	3	-	-	3
1913	Report of the Department of Fisheries of Pennsylvania	1	-	-	-	-	-	-	-	-
1914-1918	Aquarium Notes and News	11	-	-	-	-	-	-	1	1
1915	In the Open [monthly magazine]	-	-	-	1	-	-	-	-	-
1915	Proceedings of the Delware County Institute of Science	-	-	-	-	-	1	-	-	-
1915	Proceedings of the New England Zoological Club	-	-	-	-	1	-	-	-	-
1917	Bristol Daily Courier [Bristol, Bucks County, PA newspaper]	-	-	-	1	-	-	-	-	-
1917	Proceedings of the Boston Society of Natural History	1	-	-	-	-	-	-	-	-
1918	Occasional Papers of the Museum of Zoology University of Michigan	2	-	-	-	-	-	-	-	-
1918	Carnegie Institute of Washington Publication	-	-	-	-	1	-	-	-	-
1919-1933	Proceedings of the Biological Society of Washington	6	-	-	-	-	-	-	-	-
1919	Aquatic Life	1	-	-	-	-	-	-	-	-
1921-1956	Fish Culturist	120	-	1	1	-	1	-	6	1
1921-1922	Ocean City Fishing Club Year Book	2	-	-	-	-	1	-	-	-
1922-1925	American Museum Novitates	4	-	-	-	-	-	-	-	-
1922	Carnegie Institute of Washington Papers, Department of Marine Biology	1	-	-	-	-	-	-	-	-
1922	Annual Report of the Academy of Natural Sciences of Philadelphia	-	-	-	-	-	-	-	-	1
1923-1932	Occasional Papers of the Bernice P. Bishop Museum	4	-	-	-	-	-	-	-	-
1923-1928	Journal of the Bombay Natural History Society	8	-	-	-	-	-	-	-	-
1923-1958	Privately published	1	-	1	-	-	-	-	-	-
1924-1929	Yearbook of the Academy of Natural Sciences of Philadelphia	-	-	-	-	-	-	-	-	2
1924-1936	Bulletin of the American Museum of Natural History	3	-	-	-	-	-	-	-	-
1924	Memoirs of the Asiatic Society of Bengal	1	-	-	-	-	-	-	-	-
1925-1934	Annals of the Natal Museum	4	-	-	-	-	-	-	-	-
1925-1955	Bulletin of the Bernice P. Bishop Museum	3	1	-	-	-	-	-	-	-
1928-1943	Bulletin of the United States National Museum	7	-	-	-	-	-	-	-	-
1928-1949	Memoirs of the Bernice P. Bishop Museum	4	-	-	-	-	-	-	-	-
1929	Bulletin of the Maryland Conservation Department	1	-	-	-	-	-	-	-	-
1929	Proceedings of the Fourth Pacific Science Congress	1	-	-	-	-	-	-	-	-
1929	Fairmount Park Aquarium	-	-	-	1	-	-	-	-	-
1929	Report of the Fourth Pacific Science Congress	-	-	-	-	-	-	-	-	1
1930	Peking Natural History Bulletin	1	-	-	-	-	-	-	-	-
1930-1941	Hong Kong Naturalist	31	-	-	-	-	-	-	-	-
1932	Pennsylvania's Wilds and Waters	-	-	-	1	-	-	-	-	-
1935	Annals of the Transvaal Museum	1	-	-	-	-	-	-	-	-
1935	Contributions from the Charleston Museum	1	-	-	-	-	-	-	-	-
1935	Proceedings of the New England Zoological Club	1	-	-	-	-	-	-	-	-

Table 1 (continued)

Dates	Sources	Codes								
		A	B	C	D	E	F	G	H	I
1936	York Dispatch [York County, PA newspaper]	1	-	-	-	-	-	-	-	-
1937-1962	Frontiers, Academy of Natural Sciences of Philadelphia	-	-	-	2	-	-	-	-	1
1938	Report of the Board of Fish Commissioners of Pennsylvania	1	-	-	-	-	-	-	-	-
1938-1945	Monographs of the Academy of Natural Sciences of Philadelphia	3	-	-	-	-	-	-	-	-
1938	Fisheries Bulletin, Government Printing Office of Singapore	1	-	-	-	-	-	-	-	-
1939-1958	Notulae Naturae, Academy of Natural Sciences of Philadelphia	36	-	2	-	-	-	-	-	-
1940-1948	Pennsylvania Board of Fish Commissioners Bulletin	2	-	-	-	-	-	-	-	-
1941-1945	Boletin de el Museo de Historia Natural, "Javier Prado" Lima	10	-	-	-	-	-	-	-	-
1932-1941	The Aquarium	-	-	-	3	-	-	-	-	-
1941-1954	Arquivos de Zoologia do Estado de São Paulo	5	-	-	-	-	-	-	-	-
1942	Proceedings of the Eighth American Science Congress, Biological Science and Zoology	1	-	-	-	-	-	-	-	-
1942	Revista de la Academia Colombiana de Ciencias Exactas, fisica y Naturales	1	-	-	-	-	-	-	-	-
1944-1950	Pennsylvania Board of Fish Commissioners Biennial Report	6	-	-	-	-	-	-	-	-
1943-1951	Revista Chilena de Historia Natural	5	-	-	-	-	-	-	-	-
1945	*Los peces del Per*, Museo de Historia Natural "Javier Prado" Lima	1	-	-	-	-	-	-	-	-
1946	Sudan Notes and Records	1	-	-	-	-	-	-	-	-
1949	Journal of the Hong Kong Fisheries Research Station	1	-	-	-	-	-	-	-	-
1950	La Pesca	1	-	-	-	-	-	-	-	-
1951	University of California Anthropological Records	-	1	-	-	-	-	-	-	-
1952	Memorias de la Sociedad Cubana de Historia Natural	1	-	-	-	-	-	-	-	-
1952	Boletim do Instituto Paulista de Oceanografia	1	-	-	-	-	-	-	-	-
1953-1957	Queensland Department of Harbours Marine Ichthyological Notes	2	-	-	-	-	-	-	-	-
1953-1977	Quarterly Journal of the Taiwan Museum	36	-	-	-	-	-	-	-	-
1953-1955	Transactions of the Royal Society of New Zealand	3	-	-	-	-	-	-	-	-
1953	Caldasia	1	-	-	-	-	-	-	-	-
1956	Bulletin of the Research Council of Israel	1	1	-	-	-	-	-	-	-
1956-1957	New Jersey State Museum [privately printed]	2	-	-	-	-	-	-	-	-
1956	*Fishes of the Red Sea and Southern Arabia*, Weizmann Science Press of Israel, Jerusalem	1	-	-	-	-	-	-	-	-
1957	Anthropological Records	-	1	-	-	-	-	-	-	-
1958	Aquatic Life and Aquatic World	-	-	-	1	-	-	-	-	-
1959	*Fishes of Fiji*, Government of Fiji, Suva	1	-	-	-	-	-	-	-	-
1959	Bulletin of the New Jersey State Museum	1	-	-	-	-	-	-	-	-
1961	Journal of the Elisha Mitchell Scientific Society	1	-	-	-	-	-	-	-	-
	Totals	576	5	12	13	20	11	10	8	11

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NOTES

Collection numbers cited below refer to material in the Academy of Natural Sciences Archives as listed in Phillips and Phillips (1963).

[1] The Henry W. Fowler Papers (1894-1960), Collection # 117.

[2] When Fowler first became an official member of the Academy staff he served as Assistant Curator of cold-blooded vertebrates in the Department of Vertebrates. He became the first full-time caretaker of the newly formed Department of Ichthyology and Herpetology shortly before the turn of the century.

[3] Phillips and Phillips (1965) listed 609 papers by Fowler, but three papers were inadvertantly listed twice (1943b and 1943p; 1946e and 1949g; 1946f and 1949h), and Fowler's *Fishes of Chile* (1945b) is also excluded because it is a combined reprinting of three papers in Revista Chilena de Historia Natural as listed in Böhlke (1984b). An additional 64 (not 65 as stated) Fowler papers that were "previously overlooked or published posthumously," were cited by Böhlke (1984b) but of these three are not new additions: publications 1942m and 1942n (of Böhlke) were cited as 1944c and 1944d, respectively, by Phillips and Phillips (1965) and one paper (Fowler 1964) was cited in both publications (see Literature Cited herein for correct journal pagination for this paper). [The reference cited by Böhlke as Fowler 1940o should be corrected to Fowler 1934o.] Allowing for the above adjustments, the correct total number of Fowler publications is 666.

[4] The Jessup Fund was established in 1860 by the children of Augustus Edward Jessup (1796-1859) in fulfilment of his intention to provide for "the assistance of poor young men desiring to study natural history" (Nolan 1909:19). The first recipient of benefits from the Jessup endowment was the New Jersey naturalist Charles Conrad Abbott (1843-1919), who was then engaged in the study of ichthyology. Abbott, who later became better known for his contributions to the literature of nature study, published 11 ichthyological papers in the Academy's *Proceedings* (1860-1863).

[5] The Henry W. Fowler Journals, 1885-1958, (6 volumes), Collection # 199.

[6] The Henry W. Fowler Correspondence, 1894-1961, (5,519 items), Collection # 220.

[7] This sheet of instructions for collectors, Collection # 117, begins "Our Museum desires to obtain collections of marine and freshwater fishes from all parts of the World" and concludes "If you are willing to gather and preserve such materials, kindly communicate with Henry W. Fowler . . . ."

[8] In Fowler's correspondence, Collection # 220, is a letter dated 16 January 1944, from Capt. Edward L. Jackson in which he was permitted to inform Fowler that he was "somewhere in the New Hebrides." For a complete account of the fishes procurred by Jackson, see Fowler (1944b).

[9] Details of this trip are documented in Fowler's correspondence, Collection # 220. For a layman's account of the trip, see Samuelson (1984).

[10] The terms of agreement regarding exchange of duplicate Albatross Expedition specimens are detailed in a letter dated 1 April 1931 from Barton A. Bean, Collection # 220.

[11] In his unpublished "History of Ichthyology in the Academy of Natural Sciences" written in 1944 (Collection # 512), Fowler stated that six [actually seven] volumes on fishes of the Albatross Philippine Expedition had been published, and that eight more in manuscript then awaited publication.

[12] The Academy was established by a group of serious amateur naturalists for "the advancement and diffusion of useful, liberal, human knowledge." As a volunteer organization, there were no paid curators for any of the collections until the end of the nineteenth century. See "Founders Document," Collection # 527, and subsequent histories of the Academy by Nolan (1909), Phillips (1967) and Peck (1985).

[13] For brief accounts of the early history of the fish collection, see Fowler (1901:327-328, 1945:3-4) and Böhlke (1984a:3-7).

[14] The characterization of Mitchill as a "living encyclopedia" is attributed to the president of Columbia University where Mitchill taught (Kastner 1977:195). For more biographical information, see Hall (1934).

[15] Henry Fowler, personal recollections, 1959, from a tape-recorded interview with Francis Harper, in the collection of the American Philosophical Society, Philadelphia.

[16] LeSueur was considered by the renowned French ichthyologist Georges Cuvier to be the finest zoological illustrator of his day (Myers 1964:40).

[17] Maclure is reported to have given LeSueur an annual salary of $500 to pursue his studies of American fishes (Kastner 1977:197).

[18] See Böhlke (1984a:17, 83) for comments on the only extant putative types of LeSueur. The Archives of the Academy of Natural Sciences contain a number of LeSueur drawings and manuscripts (128 items), LeSueur Collection # 136.

[19] The Bonaparte Collection was purchased by Thomas B. Wilson (1807-1865), one of the most generous benefactors in the history of the Academy (Fowler 1945:16), and bequeathed to the Academy in 1872.

[20] A relatively large collection of Rafinesque's plant specimens does exist at the Academy, see Stuckey (1971) and Mears (1981).

[21] For more information on Thomas Nuttall's collecting activities on behalf of the Academy, see Graustein (1967).

[22] Cope became a member of the Academy of Natural Sciences in 1861, and received the Academy's Hayden Medal in 1891 in recognition for his work in natural history. The Hayden endowment, established in 1888 in memory of Dr. Ferdinand W. Hayden (1829-1887), made provisions for the awarding of a bronze medal "as a recognition of the best publication, exploration, discovery or research in the sciences of geology and paleontology."

[23] Henry Fowler personal reminiscences from "History of Ichthyology in the Academy of Natural Sciences," Collection # 512. For a more detailed and slightly different version of Fowler's visit to Cope's Pine Street home, see Fowler (1963).

[24] "The Hyrtl fish skeleton illustrations, 1945-1960" (139 items), Fowler Collection # 393.

[25] The Joseph Hyrtl collection of fish skeletons was bequeathed by Cope to the University of Pennsylvania and subsequently presented to the Academy in 1954. It consists of some 580 skeletons. For a detailed history of the Hyrtl Collection, see Fowler (1964:138-141 [14-17]).

[26] Letter from David Starr Jordan dated 20 February 1901 in Fowler's correspondence, Collection # 220.

[27] Fowler became incapacitated in May 1962 (V. Phillips 1964:137 [13]).

[28] Perhaps Fowler's most embarrassing error was the description (Fowler 1938b) of what he believed to be a new species of sea bass, *Pikea sericea* Fowler, based on specimens of the largemouth bass, *Micropterus salmoides* (Lacépede), a common and familiar freshwater species of eastern North America, that had been introduced to Hong Kong; see Robins and Böhkle (1960).

[29] Roughly half of the total manuscript of Fowler's *Catalog of World Fishes* was published, comprising volumes one and two and part of volume three (typed manuscript pages 764-1679); volume four (1942 pages) and volume five (722 typed pages plus about 423 handwritten pages) are in the Academy's Manuscript Collection # 712 (plus a xeroxed set in the Ichthyology Library).

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Additions to the Ichthyofauna of the Bahama Islands, with Comments on Endemic Species

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ABSTRACT.—Literature records or other documentation are given for 57 species of shorefishes added to the Bahaman ichthyofauna since publication of *Fishes of the Bahamas*; included are 32 new species described or discovered since 1967. Known distribution is specified for each species, including extralimital ranges of non-endemics. Fourteen species are listed as known only from the Bahamas although some likely occur elsewhere. It is concluded that the Bahamas has played a minor role in the evolution of Atlantic tropical marine fishes. [Bahaman ichthyofauna, endemism, new records]

With publication of *Fishes of the Bahamas* by Böhlke and Chaplin (1968), it became possible to identify over 500 species of tropical Atlantic fishes using only a single reference. This work, now long out of print, made the ichthyofauna of that vast archipelago, consisting of 260,000 sq. km and about 2750 islands, cays and exposed rocks (Wells 1988:13), the best known in the tropical Atlantic. In the more than two decades since the book was published a number of new species have been described from the Bahamas and many additional species have been taken in the area. The many new taxonomic revisions published in recent years have included range extensions and revealed the validity of several Bahaman species previously buried in synonymy. The increased use of SCUBA by scientists and observations from submersibles have also altered our knowledge of the ichthyofauna. The primary purpose of this paper is to bring together in one place all the new records of fishes of the Bahamas that have appeared since completion of the manuscript in 1967, and to provide documentation for several previously unreported species. This annotated list does not include a number of new records resulting from a series of submersible dives off San Salvador that will be documented elsewhere by R. Grant Gilmore and C. Richard Robins nor does it include several new species from the Bahamas currently under study by various investigators. In accord with restrictions of the original work we treat only shorefishes, except that all Bahaman representives of an included family are listed without arbitrary depth limitations.

METHODS AND MATERIALS

Species are listed under family headings, the families in the order of presentation in the book; genera and species are in alphabetical order within families. Recognition of families and genera generally follow Eschmeyer (1990), and common names are those recommended by the American Fisheries Society (Robins et al. 1991) or suggested by C. Richard Robins. The scientific name, author, and common name are

given, followed by a brief distributional discussion. New species described or discovered since the book was published are indicated by an asterisk. References preceding the discussion document the occurrence of the species in the Bahamas, and references cited in the discussion provide additional information, usually extralimital distributional data. If the initial reference is not the primary identification source for the species, one for that purpose is given in brackets after the discussion. If no documentary literature reference exists, known specimens are listed with their museum catalog numbers (abbreviations for institutional depositories are: American Museum of Natural History, AMNH; Academy of Natural Sciences of Philadelphia, ANSP), number of specimens, size or size range (in mm standard length) and locality data.

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We acknowledge the assistance of the following colleagues who have worked on fishes of the Bahamas and the Caribbean in the intervening years, and who have reviewed our list: Patrick L. Colin, Florida State University Marine Laboratory; Carter R. Gilbert, Florida Natural History Museum; C. Richard Robins, University of Miami, Rosenstiel School of Marine and Atmospheric Sciences; and C. Lavett Smith, American Museum of Natural History.

ADDITIONS TO BAHAMAN ICHTHYOFAUNA

Family Dasyatidae
Stingrays

Himantura schmardae (Werner)
Caribbean stingray

Material examined.—ANSP 103787 (1, 735 mm greatest disc width); Great Exuma Island; B.Minns; July 1968. ANSP 114087 (1, 352 mm GDW); Flats off south side Great Exuma Island; B.Minns; Sept. 1968.

Böhlke (1969b:19) The occurrence of the Caribbean stingray in the Bahamas has previously been reported only in a popular account; elsewhere known from Suriname, Trinidad, Cuba, Jamaica, Mexico and the western Caribbean. [Bigelow and Schroeder 1953:394]

Family Muraenidae
Morays

***Enchelycore carychroa** Böhlke & Böhlke
Chestnut moray

Böhlke and Böhlke (1976:138) The species illustrated and described on p. 81 in *Fishes of the Bahamas* as *Enchelycore* sp. is this species. An insular species, common on coral reefs throughout the Bahamas; elsewhere found in islands of the Caribbean and off Central and South America, in Bermuda and the Florida Keys.

Family Ophichthidae
Snake eels

Ophichthus gomesii (Castelnau)
Shrimp eel

McCosker et al. (1989:391) The species illustrated and described on p. 104 in *Fishes of the Bahamas* as *Ophichthus* sp. is this species. Only one small specimen taken off Great Exuma (Great Bahama Bank); a common species usually taken by trawl in coastal United States waters from South Carolina south and throughout the northern Gulf of Mexico, also off Brazil; infrequently found in the West Indies.

Family Poeciliidae
Livebearers

Gambusia hubbsi Breder
Bahama gambusia

Breder (1934) Found in fresh and brackish waters throughout the Bahamas, except some inland lakes on New Providence Island where

apparently only *Gambusia manni* occurs; see also discussion of "Endemic Bahama Species" below.

Poecilia latipinna (Lesueur)
Sailfin molly

Material examined.—ANSP 126930 (1, 34.5); New Providence, Lake Cunningham, SW to SE shore, to 0.3 m; J.E. Böhlke et al.; 24 Aug. 1972.

Known from salt, brackish and fresh waters, from North Carolina south to Florida and Cuba, and along the Gulf coast south to Yucatán. [Rosen 1973:241]

Family Anomalopidae
Flashlight fishes

Kryptophanaron alfredi Sylvester
Caribbean flashlight fish

McCosker (1982:97) This nocturnally active fish, which has been observed only on steep dropoff habitats, has previously been reported from the Bahamas only from San Salvador on the Great Bahama Bank, but has also been collected from the Exumas and Conception Is. (P.L. Colin, in litt.); elsewhere it has been reported from Jamaica, Grand Cayman Island, Puerto Rico and Curacao. [Colin et al. 1979]

Family Bythitidae
Viviparous brotulas

*****Lucifuga spelaeotes*** Cohen & Robins
Bahaman cavefish

Cohen and Robins (1970:135) A Bahaman endemic, *Lucifuga spelaeotes* was described from sinkhole pools on New Providence Island in the Great Bahama Bank; see also discussion of "Endemic Bahaman Species" below.

Family Syngnathidae
Pipefishes

*****Anarchopterus tectus*** (Dawson)
Insular pipefish

Dawson (1982a:38) Taken from New Providence area of the Great Bahama Bank; elsewhere known from the Florida Keys, and the Caribbean Sea south to Venezuela.

Family Bothidae
Lefteye flounders

*****Bothus robinsi*** Topp & Hoff
Twospot flounder

Topp and Hoff (1972:62) The species illustrated and described on p. 216 in *Fishes of the Bahamas* as *Bothus* sp. is this species. In the Bahamas taken at two localities on the Great Bahama Bank; elsewhere known from Bermuda, North Carolina south to Rio de Janerio, and the northern Gulf of Mexico.

Family Apogonidae
Cardinalfishes

*****Apogon leptocaulus*** Gilbert
Slendertail cardinalfish

Dale (1977:28) In the Bahamas from Eleuthera in the Great Bahama Bank and from Mayaguana Island; elsewhere known from the east coast of Florida, and the western Caribbean (Providencia Island and Glovers Reef). [Gilbert 1972a:421]

*****Apogon mosavi*** Dale
Dwarf cardinalfish

Dale (1977:20) In the Bahamas from the Great Bahama and Little Bahama banks, and from San Salvador (C.R. Gilbert, pers. comm.); elsewhere known from Haiti and Jamaica.

Family Serranidae
Sea basses

Epinephelus (Dermatolepis) inermis (Valenciennes)
Marbled grouper

Material examined.—AMNH 30976 (1, 664); north Bimini, west side, 122 m; Captain J. Heley; 1 Apr. 1972.

Elsewhere known from southern Florida, Cuba, Puerto Rico, Jamaica, Lesser Antilles, and Brazil. [Smith 1971:158]

Hypoplectrus chlorurus (Valenciennes)
Yellowtail hamlet

Material examined.—ANSP 121760 (1, 73.4); Cat Island, SW end off Hawksnest Creek just south of Hawksnest Point, 27-29 m; J.C. Tyler, C.L. Smith; 31 Jan. 1968.

Elsewhere known from the Gulf of Mexico, West Indies and Venezuela. The above record brings to seven the nominal species of *Hypoplectrus* known from the Bahamas. Some authors (Graves and Rosenblatt 1980; Robins et al. 1980:81) believe that all Atlantic *Hypoplectrus* are color morphs of a single species (*H. unicolor*). For convenience, and in conformity with *Fishes of the Bahamas*, we continue to recognize the distinctive color morphs of *Hypoplectrus* as valid species. [Randall 1968a:73, fig. 82]

Liopropoma aberrans (Poey)
Eyestripe bass

Robins (1967:591) This relatively deep-water *Liopropoma* is known only from south of Great Inagua Island and from the Tongue-of-the-Ocean (Colin 1976:604) in the Bahamas, and from Cuba, Jamaica and Belize (Colin 1974:34).

Paranthias furcifer (Valenciennes)
Creole-fish

Smith (1971:87) In the Bahamas taken at Turks Island and sighted at Acklins Island (C.L. Smith, pers. comm.); elsewhere known from Bermuda and Florida south to Brazil.

Serranus luciopercanus Poey
Crosshatch bass

Colin (1976:604) Published Bahaman record based on sightings from a submersible at depths of 105-140 meters on the northern margin of the Tongue-of-the-Ocean; elsewhere known from Cuba, Grand Cayman Island, Jamaica, Honduras, Martinique and Puerto Rico. [Robins and Starck 1961:282]

Family Grammatidae
Basslets

*****Gramma linki*** Starck & Colin
Yellowcheek basslet

Starck and Colin (1978:147) Taken in the Bahamas from the Little Bahama, Great Bahama, and Cay Sal banks; also found in the West Indies and along the Mexican and Central American coasts.

*****Lipogramma evides*** Robins & Colin
Banded basslet

Gilmore and Jones (1988:441) From San Salvador in the Bahamas; elsewhere from Arrowsmith Bank, Barbuda and Jamaica. [Robins and Colin 1979:41]

*****Lipogramma flavescens*** Gilmore & Jones
Yellow basslet

Gilmore and Jones (1988:436) Only the holotype from San Salvador known; a relatively deepwater species taken in 285 m.

Lipogramma klayi Randall
Bicolor basslet

Robins and Colin (1979:51) Collected in the Berry Islands of the Great Bahama Bank at a depth of 45 m; also taken in Puerto Rico, Jamaica, Belize and Curacao.

Lipogramma regium Robins & Colin
Royal basslet

Robins and Colin (1979:48) Known only from Andros Island in the Great Bahama Bank, and southwestern Puerto Rico. The spelling of the trivial name has been modified from that given in the original description following Gilmore and Jones (1988:437).

Family Priacanthidae
Bigeyes

Pristigenys alta (Gill)
Short bigeye

Starnes (1988:138) One specimen taken at Grand Bahama Island, Little Bahama Bank; elsewhere found throughout the western Atlantic along the east coast of North America, the Caribbean and the Gulf of Mexico.

Family Malacanthidae
Tilefishes

Caulolatilus dooleyi Berry
Bahama tilefish

Berry (1978:56) Known only from the Bahamas where taken off Bimini, from the south side of Tongue-of-the-Ocean, and from Caicos Bank in 166-256 m.

Caulolatilus williamsi Dooley & Berry
Yellow-bar tilefish

Dooley and Berry (1977:10) Taken in the Bahamas off Cay Sal Bank, and off St. Croix, Virgin Islands in 125-220 m.

Family Chaetodontidae
Butterflyfishes

Chaetodon guyanensis Durand
Guyana butterflyfish

Colin (1976:604) Bahaman record based on sightings from a submersible at depths of 110-230 m on the northern margin of the Tongue-of-the-Ocean; elswhere known from Puerto Rico, Jamaica, Barbados, Belize and French Guiana. [Hubbs 1963:161; Burgess 1978:338]

Family Pomacentridae
Damselfishes

Chromis enchrysura Jordan & Gilbert
Yellowtail reeffish

Colin (1976:604) Bahaman records of this species are based on submersible sightings of "bicolor damselfish" off the northern margin of the Tongue-of-the-Ocean in depths of 109-116 m; elsewhere known from Bermuda, North Carolina to Florida, Puerto Rico, western Caribbean, Guyana and Brazil. [Emery and Smith-Vaniz 1982:158]

Chromis scotti Emery
Purple reeffish

Colin (1976:604) Bahaman records based on sightings from a submersible in 108 m on the northern margin of the Tongue-of-the-Ocean, and from an unspecified locality (Gilbert 1972b:138); we have also examined specimens (ANSP 149417) collected in 45 m from the Nassau area. Elsewhere this damselfish is known from Bermuda, North Carolina to Florida, Jamaica, Belize, Colombia and Curacao. [Emery 1968:49]

Stegastes diencaeus (Jordan & Rutter)
Longfin damselfish

Greenfield and Woods (1974:9, as *Eupomacentrus diencaeus*) The illustration and

account of *Eupomacentrus* sp. on p. 435 in *Fishes of the Bahamas* is of this species. Taken at Plana Cays, Mayaguana, and Athol Island in the Great Bahama Bank; elsewhere known from Haiti, Anguilla, and off Belize. [Robertson and Allen 1981]

Family Labridae
Wrasses

Decodon puellaris (Poey)
Red hogfish

Colin (1976:604) Bahaman records based on sightings at a depth of 155 m on the northern margin of the Tongue-of-the-Ocean; elsewhere in the western Atlantic known from Bermuda and off South Carolina south to Brazil. [Gomon 1974:214]

Family Opistognathidae
Jawfishes

***Opistognathus megalepis** Smith-Vaniz
Largescale jawfish

Smith-Vaniz (1972:48) This deep-water Bahaman jawfish has been trawled at depths of 198-301 m in the Northwest Providence Channel off Grand Bahama Island; elsewhere known from Arrowsmith Bank off Yucatan and the Lesser Antilles.

***Opistognathus** n.sp.
Spotfin jawfish

Material examined.—AMNH 28297 (1, 59.3); Little Bahama Bank, Abaco Bight, Mangrove Cay; C.L. Smith et al.; 6 Dec. 1966.

This new species of jawfish, which will be formally described by William F. Smith-Vaniz and Patrick L. Colin, is also known from South Carolina to the Florida Keys and the Gulf of Mexico to Texas.

***Opistognathus** n.sp.
Roughcheek jawfish

This new species, also being described elsewhere by Smith-Vaniz and Colin, has been collected by submersible in a series of dives of 249-300+ m off San Salvador; also known from the Lesser Antilles.

Family Dactyloscopidae
Sand stargazers

***Dactyloscopus boehlkei** Dawson
Shortchin stargazer

Dawson (1982b:29, 40) The illustration and account of *Dactyloscopus poeyi* Gill on p. 497 in *Fishes of the Bahamas* were based on specimens of this new species, although some specimens of *D. poeyi* were also included (see Dawson for separation of the species). Known only from shallow waters in the Bahamas, in the Great Bahama Bank and Plana Cays.

Dactyloscopus poeyi is known from the Cay Sal and Great Bahama banks, the Antilles, and in the western Caribbean Sea from Belize to Venezuela.

***Dactyloscopus comptus** Dawson
Eyespot stargazer

Dawson (1982b:34) Taken in the Bahamas in Little Bahama and Great Bahama banks; two questionable specimens from Puerto Rico and St. John, Virgin Islands.

***Platygillellus smithi** Dawson
Sailfin stargazer

Dawson (1982b:67) Only the holotype from shallow waters (0-8 m) off Little Inagua Island known.

Family Labrisomidae
Labrisomids

Labrisomus filamentosus Springer
Quillfin blenny

Material examined.—ANSP 134509 (1, 70.7); Berry Islands, south side of Whale Cay, 21 m; P.L. Colin; 28 Mar. 1973. ANSP 138126 (1, 104.4); Little Inagua Island, SW side, 15-30 m; L.B. Williams; 18 Apr. 1977.

Elsewhere known from Hispanola, Virgin Islands, and the western Caribbean off Honduras and Nicaragua (Springer and Rosenblatt 1965:27). [Springer 1959]

***Nemaclinus atelestos** Böhlke & Springer
Threadfin blenny

Böhlke and Springer (1975:58) Bahaman specimens from Great Bahama Bank; elsewhere known from off Bermuda, Argus or Challenger Bank (USNM 175785), throughout the Antilles and in the northern Gulf of Mexico.

***Starksia elongata** Gilbert
Elongate blenny

Gilbert (1971b:195) From the southern Bahama Islands; elsewhere known from Providencia Island and Glovers Reef off Belize (Greenfield and Johnson 1981:95).

Starksia hassi Klausewitz
Ringed blenny

Gilbert (1971b:204) Bahaman specimens from West Plana Cay and Little San Salvador; also reported from the Antilles, South America and Glovers Reef off Belize (Greenfield and Johnson 1981:95). [Böhlke and Springer 1961:35]

Family Chaenopsidae
Pikeblennies

***Emblemariopsis occidentalis** Stephens
Redspine blenny

Stephens (1970:287) The species illustrated and described on p. 547 in *Fishes of the Bahamas* as *Pseudemblemaria signifera* (Ginsburg) is this species. In the Bahamas from the Great Bahama Bank; elsewhere found at Grand Cayman, Providencia Island and the Lesser Antilles.

In the Bahamas *Emblemariopsis signifera* has been recorded from New Providence Island, Great Bahama Bank; elsewhere it occurs throughout the West Indies and off the coasts of Honduras, Belize, Colombia, and Brazil (Greenfield and Johnson 1981:65).

Family Gobiidae[1]
Gobies

Coryphopterus lipernes Böhlke & Robins
Peppermint goby

Smith and Tyler (1977:5) In the Bahamas found in the Great Bahama, Little Bahama and Caicos banks; described from the Florida Keys, found also in the Virgin Islands, Grand Cayman Island, Jamaica, Belize, Providencia Island, and Curacao. [Böhlke and Robins 1962:186]

***Evermannichthys convictor** Böhlke & Robins
Tenant goby

Böhlke and Robins (1969:11) A sponge-dwelling species, described from Green Cay, Great Bahama Bank; also known from Haiti (Gilbert and Burgess 1986:161).

[1]*Coryphopterus tortugae* (Jordan), recently redescribed by Garzón and Acero (1990:105) as a valid species, has long been considered a pallid form of *Coryphopterus glaucofraenum* Gill by many authors (Longley and Hildebrand 1941:232; Böhlke and Robins 1960:107; Böhlke and Chaplin 1968:595). We have reexamined our Bahaman material and other recently collected specimens of *C. glaucofraenum* and find the characters used by Garzón and Acero to separate the two nominal species (body depth, head pigmentation and basicaudal marks) highly variable and correlated with specimen size (body depth) and/or substrate coloration. We consider *C. tortugae* to be a synonym of *C. glaucofraenum*.

Evermannichthys silus Böhlke & Robins
Pugnose goby

Böhlke and Robins (1969:10) A sponge-dwelling species, known only from Samana Cay, east of the Great Bahama Bank.

****Gobiosoma atronasum*** Böhlke & Robins
Blacknose goby

Böhlke and Robins (1968:88) Known only from Exuma Sound in the Great Bahama Bank; see also discussion of "Endemic Bahaman Species" below. [Colin 1975:142]

Gobiosoma chancei Beebe & Hollister
Shortstripe goby

Material examined.—ANSP 112629 (2, 24.0-34.7), ANSP 112630 (1, 29.7) and ANSP 112631 (1, 29.0); Long Island, 11 m; J.C. Tyler; 13 Jan. 1968. ANSP 112632 (1, 35.8), ANSP 112633 (3, 30.6-32.1), ANSP 112634 (2, 15.5-38.7), ANSP 112635 (1, 40.2) and ANSP 112636 (1, 32.8); Great Inagua, 15 m; J.C. Tyler; 18 Jan. 1968. ANSP 112637 (2, 27.6-38.4); locality as preceding, 20 m; J.C. Tyler, 19 Jan. 1968. ANSP 112638 (1, 26.8); Little Inagua, 21 m; J.C. Tyler; 21 Jan. 1968. ANSP 112639 (2, 22.2-36.7); locality as preceding, 18-24 m; J.C. Tyler; 21 Jan. 1968. ANSP 112640 (2, 32.0-38.9); Plana (French) Cays, 27 m; J.C. Tyler; 26 Jan. 1968. ANSP 112641 (7, 27.4-42.6); Samana (Atwood) Cay, 20 m; J.C. Tyler; 27 Jan. 1968. ANSP 112642 (1, 37.4); Samana (Atwood) Cay, 20 m; J.C. Tyler; 28 Jan. 1968. ANSP 112643 (6, 31.1-42.5); Samana (Atwood) Cay, 17-34 m; J.C. Tyler; 28 Jan. 1968. ANSP 134511 (1, 37.7); southern Bahamas; P.L. Colin.

Known from islands only in the southern Bahamas, and from Los Testigos and the Gulf of Cariaco off northern Venezuela. [Colin 1975:82].

Lythrypnus crocodilus (Beebe & Tee-Van)
Mahogany goby

Greenfield (1988:465) Known from the southern Bahama Islands; also occurs in the Greater and Lesser Antilles, and the western Caribbean (Belize, Honduras and Providencia Island off Nicaragua).

****Lythrypnus minimus*** Garzón & Acero
Pygmy goby

Material examined.—ANSP 92885 (1,9.4); N. of Green Cay, 25°07'06"N, 77°11'32"W; C.C.G. Chaplin, J.E. Böhlke, C.R. Robins, B. Parker; 14 Nov. 1960.

The photographed specimen on p. 625 in *Fishes of the Bahamas*, thought to be an exceptionally banded individual of *Lythrypnus elasson* Böhlke and Robins, is this species (Garzón and Acero 1988:309). Due to previous confusion with *L. elasson* the distribution of this diminutive goby (sexually mature females are 7.5-10.0 mm SL) is not well established. In addition to the single Bahaman record cited above, *L. minimus* is known from Providencia Island in the western Caribbean and from the north coast of Colombia.

****Pariah scotius*** Böhlke
Peppered goby

Böhlke (1969a: 3) Described from Mayaguana, Great and Little Inagua, and Conception Islands in the southern Bahamas; also known from Haiti (ANSP 126260).

****Varicus imswe*** Greenfield
Whiteband goby

Williams and Gilbert (1983:186) Known from Eleuthera Island in the Great Bahama Bank, and from Belize. [Greenfield 1981:269]

****Vomerogobius flavus*** Gilbert
Lemon goby

Gilbert (1971a:35) Known only from Eleuthera Island in the Great Bahama Bank and from islands in the southern Bahamas.

Family Microdesmidae
Wormfishes

Ptereleotris helenae (Randall)
Hovering goby

Material examined.—ANSP 134510 (1, 29.7) Andros Is.; Fresh Creek, ca. 1/4 mi. NE off Goat Cay; TORITO sta. 23; J. D. Starck and P. Hopper; 21 Dec. 1969.

Broadly distributed throughout the West Indies. [Randall 1968b:108, as *Ioglossus helenae*; *Ioglossus a* synonym of *Ptereleotris* in Eschmeyer, 1990:199]

Family Triglidae
Searobins

Bellator egretta (Goode & Bean)
Streamer searobin

Miller and Richards (1991a:642) Reported from the Bahamas off San Salvador based on sightings from a submersible; elsewhere known from North Carolina south to Barbados, and the southeast Gulf of Mexico, in 82-205 m.

Prionotus murielae Mowbray
Threadfin searobin

Mowbray *in* Borodin (1928:26) This searobin, which differs from all other western Atlantic species of *Prionotus* in having the upper two pectoral fin rays filamentous, is known only from the holotype taken on Cay Sal Bank in 11 m; Miller and Richards (1991b:757), quoting an unpublished manuscript by Issac Ginsburg, give a detailed redescription and comparison with *P. ophryas* Jordan and Swain.

Family Scorpaenidae
Scorpionfishes

Pontinus nematophthalmus (Günther)
Spinythroat scorpionfish

Eschmeyer (1969:28) A deepwater species (82-412 m) taken in the Northwest Providence Channel; elsewhere known from Florida, throughout the Caribbean and south to Brazil.

Pontinus castor Poey
Longsnout scorpionfish

Eschmeyer (1969:31) Taken south of Great Inagua and in the Northwest Providence Channel in 41-128 m; also known from Bermuda, Cuba, north of Puerto Rico, and the Virgin Islands.

Neomerinthe beanorum (Evermann & Marsh)
Spotwing scorpionfish

Eschmeyer (1969:43) Trawled in 216-384 m on the Bahaman side of the Straits of Florida; also known from throughout the Caribbean.

Family Gobiesocidae
Clingfishes

Derilissus nanus Briggs
Dwarf clingfish

Briggs (1969:333) Previously known only from West Plana Cay in the southern Bahamas, this clingfish has also been collected at Eleuthera Island, Great Bahama Bank (P.L. Colin, in litt.).

ENDEMIC BAHAMAN SPECIES

Twenty three of the 26 species reported as known only from the Bahamas by Böhlke and Chaplin in 1968 have subsequently been collected elsewhere in the Caribbean. The remaining three plus ten of the additional species listed above are presently known only from the Bahamas, but some almost certainly are not Bahaman endemics. Some of these species occur in restricted, poorly sampled habits (e.g., *Dactyloscopus boehlkei* and *Platygillelus smithi*) or are deep-water species (e.g., *Caulolatilus dooleyi* and *Lipogramma flavescens*), also infrequently sampled. Of the remaining species listed below, some also may not be confined to the Bahamas. If they are true endemics, the factors responsible for their limited distributional patterns require explanation (except *Gobiosoma atronasum*, see below).

Despite its rich ichthyofauna it is apparent that the Bahamas has not played a major role in the evolution of tropical Atlantic fishes because, excluding the first three families (whose species are confined to inland ponds and sink holes), less than one percent of Bahaman species are endemics.

Family Cyprinodontidae
Killifishes

Cyprinodon laciniatus Hubbs & Miller
Bahama pupfish

Hubbs and Miller (1942:5) This pupfish is known only from lakes on New Providence Island, Great Bahama Bank.

Cyprinodon spp.

Two or three undescribed species are known only from the San Salvador area (R.G. Gilmore, pers. comm.).

Family Poeciliidae
Livebearers

Gambusia manni Hubbs
New Providence gambusia

Hubbs (1927:61) Apparently limited to two land-locked brackish lakes on New Providence Island, Lakes Cunningham and Killarney (Fink 1971:28).

Gambusia hubbsi Breder

Breder (1934) Described from Andros Island, this gambusia is widespread throughout the Bahamas apparently exclusive of the two localities on New Providence Island where *G. manni* occurs (Rauchenberger 1989:62).

The precise taxonomic status of the above two species of *Gambusia* is equivocal. Following Rosen and Bailey (1963:98), most authors have considered *G. hubbsi* to be a synonym of *G. manni*. However, Fink (1971) recognized both *G. manni* and *G. hubbsi* (and six other forms) as subspecies of *G. puncticulata* Poey (as *G. puncticulata manni* and *G. p. puncticulata*, respectively), primarily because they were not gonopodially distinct and, combined as nominal subspecies, had overlapping ranges for all the characters studied. On the basis of additional characters, including electrophoretic analysis, Greenfield and Wildrick (1984) recognized three sub-groups within the *puncticulata* species group, but the taxonomic status of the various populations comprising the "*hubbsi*" complex (consisting of three isolated Cuban forms, one from Hispaniola, and the two nominal Bahaman species) was not investigated. Most recently, Rauchenberger (1989:52, 60 and Fig. 57) provisionally recognized two Bahaman species of *Gambusia*, after acknowledging that further "alpha-level work" needed to be done to address species problems. She noted that within the monophyletic "*hubbsi* group" (including *G. manni*), only *G. hubbsi* and *G. hispaniolae* Fink have the hypural fused into a single plate with a keyhole.

Family Bythitidae
Viviparous brotulas

Lucifuga spelaeotes Cohen & Robins

Cohen and Robins (1970:135) This species, believed to be the most primitive of the three recognized species of *Lucifuga* (the other two are both Cuban species), is now known from three Bahaman localities; in addition to the type locality, Mermaid's Pool on New Providence Island, it has been taken at Lucayan Cavern on Grand Bahama Island and from an inland sink hole on Great Abaco, Little Bahama Bank.

Family Gobiidae
Gobies

Evermannichthys silus Böhlke & Robins

Böhlke and Robins (1969:10) One of four species of *Evermannichthys* (all specialized obligate sponge-dwellers), *E. silus* is known only from Samana Cay based on a single collec-

tion taken from two "stinking sponges" (subsequently identified as *Ircinia strobilina*) found at a depth of 27 m.

Gobiosoma atronasum Böhlke & Robins

Böhlke and Robins (1968:88) Known only from Exuma Sound, *G. atronasum* may owe its differentiation and apparent limited distribution to an isolated refugia there during low sea levels associated with Pleistocene glaciation (Colin 1975:274-275).

Gobiosoma evelynae Böhlke & Robins
Sharknose goby

Although not an endemic species, this cleaning goby has three distinctive color forms, one of which is restricted to the Bahamas (Colin 1975:32-39); the "yellow form," see plate 34b in *Fishes of the Bahamas*, occurs only in the northern Bahamas (Exuma Sound to the eastern Little Bahama Bank). The total range of *G. evelynae* is throughout the Bahamas, the Antilles, western Caribbean and northern South America.

Vomerogobius flavus Gilbert

Gilbert (1971a:35) This small goby (16.0-20.7 mm SL) is still known only from the Bahamas (C.R. Gilbert, pers. comm.), see above. The restricted habitat (steep drop-off habitats) and diminutive size of this goby and the following clingfish may explain why they have not been discovered elsewhere, but P.L. Colin (in litt.) has spent many years searching in appropriate habitats for both species and has found them only in the Bahamas.

Family Gobiesocidae
Clingfishes

Derilissus nanus Briggs

Briggs (1969:333) This tiny clingfish (gravid females are 11.3-14.0 mm SL) is known only from two localities in the Bahamas (see above).

Gobiesox lucayanus Briggs
Bahama skilletfish

Briggs (1963:604) In the Bahamas known only from New Providence Island, the Exuma Cays and Little Inagua. That this shallow water (< 3 m) species has not been collected in Hispanola or Cuba is surprising.

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ERRATA

In some copies of volume 142 (for 1990) of the *Proceedings*, part of the literature cited (last page) is missing from the paper by Scott A. Schaefer "Anatomy and Relationships of the Scoloplacid Catfishes" that begins on page 167. The entire missing page is given below.

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